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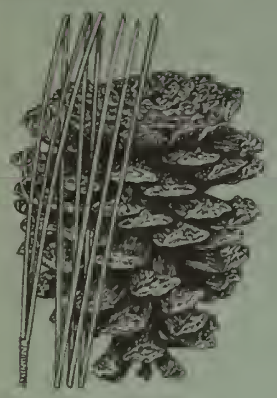
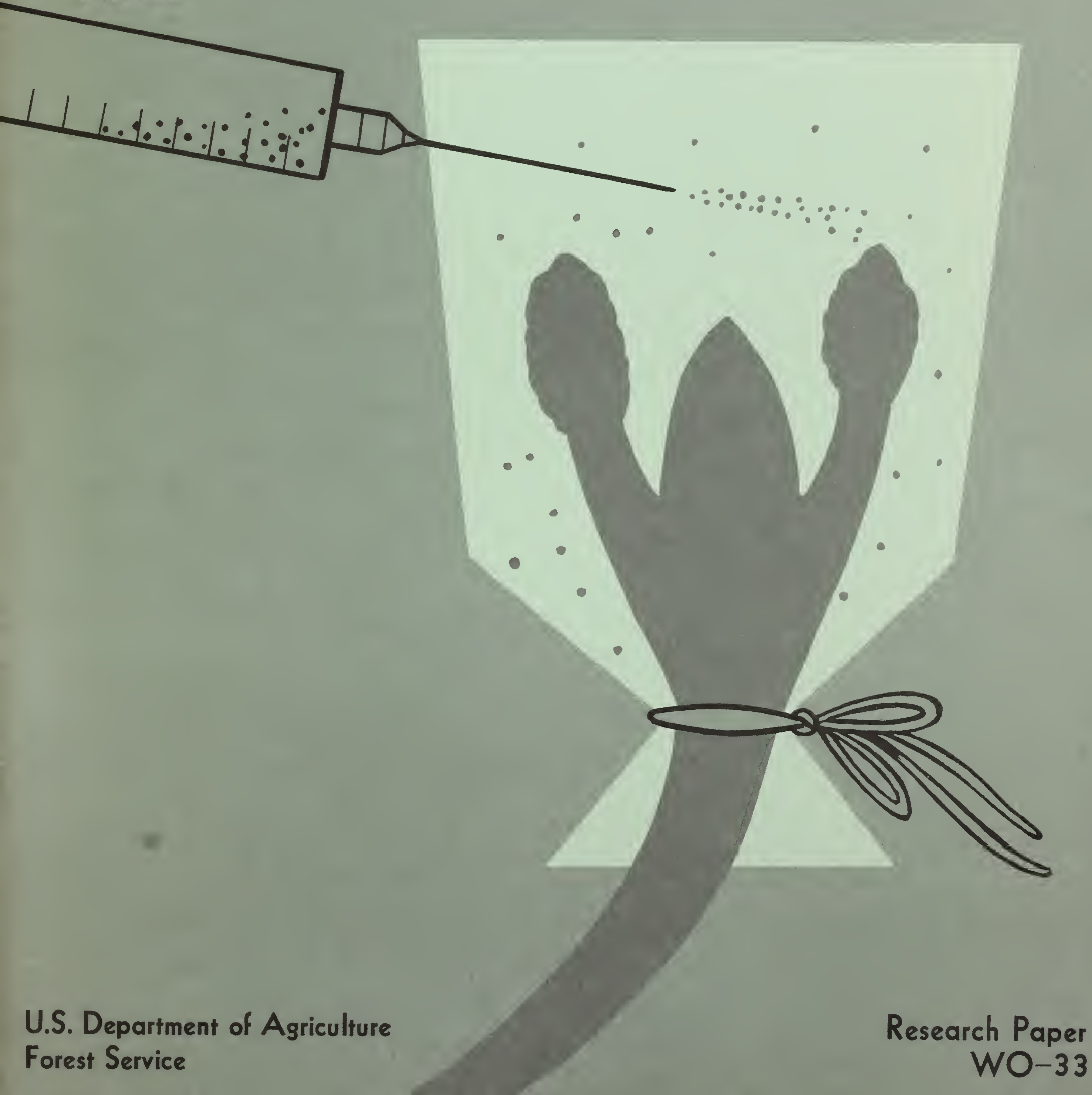
GENETICS



OF LONGLEAF PINE



U.S. Department of Agriculture
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WO-33

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CONTENTS

Page

RESEARCH SUMMARY ii

INTRODUCTION 1

SEXUAL REPRODUCTION 3
  Reproductive Development 3
  Cross- and Self-Pollination 4
  Controlled Pollination 4
  Seed Handling 4

ASEXUAL REPRODUCTION 5
  Rooting 5
  Grafting 5

VARIATION AND INHERITANCE 6
  Survival and Growth 6
  Resistance to Pests and Environmental Stress 8
  Form and Crown Characteristics 10
  Wood Properties and Naval Stores 10
  Mutant Forms 11

INTERSPECIFIC HYBRIDIZATION 11
  Longleaf × Loblolly Pine Hybrids 13
  Longleaf × Slash Pine Hybrids 13
  Longleaf × Shortleaf Pine Hybrids 15

IMPROVEMENT PROGRAMS 15
  Procedures 15
  Seed Orchards 16

RESEARCH NEEDS 17

LITERATURE CITED 18

RESEARCH SUMMARY

Though long in disfavor with practicing foresters, longleaf pine has an important place in southern forestry. The species possesses an array of desirable traits not easily obtained in other southern pines. The wood is particularly valuable for high value products such as poles, piling, and other solid wood products.

Longleaf pine is classified along with the other major southern pines and seven related species in Subsection *Australes*. Natural or artificial hybrids with loblolly, slash, and shortleaf pines have been reported. The hybrid with loblolly pine—*Pinus* × *sondereggeri* H. H. Chapm.—was the first reported and only named southern pine hybrid.

Both male and female strobili occur on the same tree. The species is wind-pollinated and normally outcrossing, but some natural selfing occurs. Seed yields generally are adequate but vary widely among individual trees, areas, and years. The large, conspicuous strobili were used to develop techniques for controlled pollination of southern pines. Controlled pollinations are effected with relative ease. Seed are damaged easily and must be extracted, cleaned, and stored carefully. Grafting is the most reliable means of asexual propagation.

Unlike related species, newly germinated or planted longleaf pine remains in a stemless grass stage for several growing seasons. Regeneration problems caused by delayed height growth and poor survival are compounded by brown-spot needle blight. Recent advances in nursery and planting technology largely offset such problems, and prospects for improving survival, growth, form, and pest resistance via selection and breeding are attractive.

Variation among seed sources in important traits is substantial. Results from rangewide provenance tests indicate that trees from coastal areas generally outperform those from inland areas at all but the coldest planting locations. Therefore, considerable improvement can be achieved over much of the species range by using seed from the central Gulf Coast.

Variation among individual trees exceeds that among seed sources. Occasional parent trees produce offspring that grow several times faster than the average. Heritabilities established from progeny tests are varied but generally high enough to make breeding programs profitable. Correlations among traits are such that yield can be improved without adverse effects on form and other traits. Recommended improvement procedures include proper choice of seed source and short-term progeny testing before seed orchard establishment. Such procedures are especially effective for improving survival, early growth, and resistance to brown-spot needle blight—traits of paramount importance in this species. Seedling seed orchards also appear useful from this standpoint.

GENETICS OF LONGLEAF PINE

E. Bayne Snyder, Ronald J. Dinus, and Harold J. Derr[1]

INTRODUCTION

Pinus palustris Mill., commonly called longleaf pine, is an important member of the group known commercially as southern yellow pines. Unlike related species, young longleaf pines typically remain in a stemless grass stage for several growing seasons (Wahlenberg 1946). This inherent pattern of growth, possibly an adaptation for fire resistance, has complicated artificial regeneration. Once past the grass stage, however, longleaf grows as fast as the other pines and offers desirable characteristics that make it suitable for high value products. Hence, improvement efforts are important to southern forestry, and the species ranks fifth nationally in seed orchard area (USDA Forest Service 1974a).

Longleaf pine is in the Subsection *Australes,* which contains 11 species, 8 in the southeastern United States, 2 in the West Indies, and 1 common to the West Indies and Central America (Little and Critchfield 1969). The number of related species with overlapping ranges has provided ample opportunity for interspecific hybridization. Natural or artificial hybrids have been reported with at least three species.

Longleaf pine was the first southern species favored for commercial use (Wahlenberg 1946). Vast, almost pure stands once occurred in a wide band along the Coastal Plain from Virginia to Texas and extended northward into the mountains of Alabama and Georgia (fig. 1).

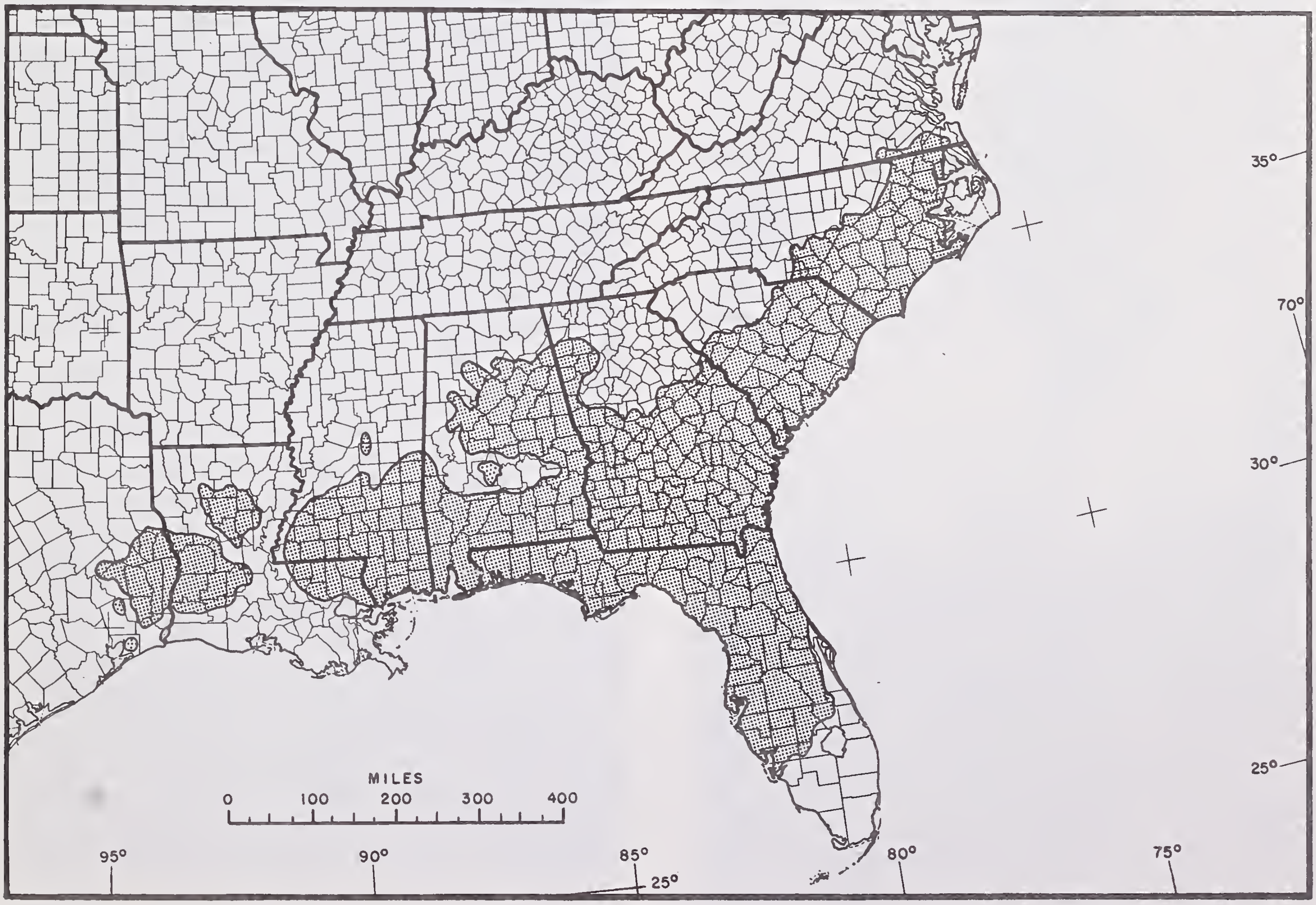

Figure 1.—Natural range of longleaf pine.

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These extensive stands were easily exploited, and near total removal devastated much of the resource, leaving only scattered trees or sparse stands to supply seed for natural regeneration. In addition, large areas were cleared for farming. By 1930, the volume of longleaf pine was estimated at one-tenth the original.

Cutover lands and abandoned fields were quickly occupied by the more prolific and easily regenerated loblolly (*P. taeda* L.) and slash (*P. elliottii* Engelm. var. *elliottii*) pines. Planting became a preferred means of restoring the depleted forest resource (Wakeley 1954), and loblolly and slash pine were favored over longleaf pine because of their ease of planting and rapid early growth. Exclusion of wildfire further facilitated wider use of these species.

Despite nearly complete replacement in many areas, longleaf pine remains important for a variety of products. The species possesses many desirable qualities not common to or easily obtained in rival species. Most trees are well-formed, straight, and free of branches over much of their boles (fig. 2). These attributes and the naturally high bolewood density make longleaf a preferred species for poles, piling, structural timber, and other high value products. Quality and quantity of oleoresin yields approach those of slash pine.

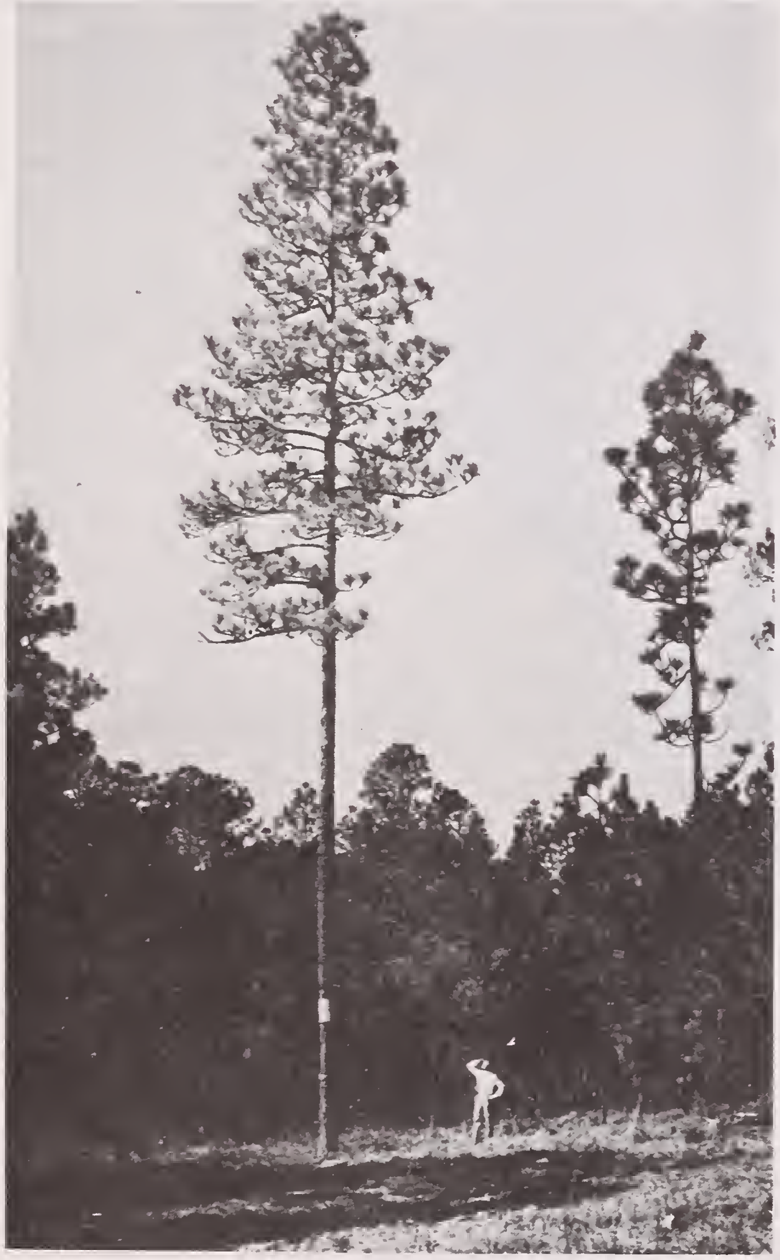

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Figure 2.—A longleaf pine of superior growth and form.

Longleaf pine is seldom damaged severely by fire, ice, or windthrow. The most important pest of longleaf pine is brown-spot needle blight (*Scirrhia acicola* (Dearn.) Sigg.), a disease that defoliates seedlings. Some degree of control is possible with fungicides and prescribed burning, but breeding for resistance is an important aim in improvement programs. Management is not complicated seriously by other disease and insect pests. The species is largely resistant to fusiform rust (*Cronartium fusiforme* Hedgc. & Hunt ex Cumm.) (Siggers 1955), an important disease of loblolly and slash pines.

Recent advances in nursery and regeneration practices suggest that the primary deterrents

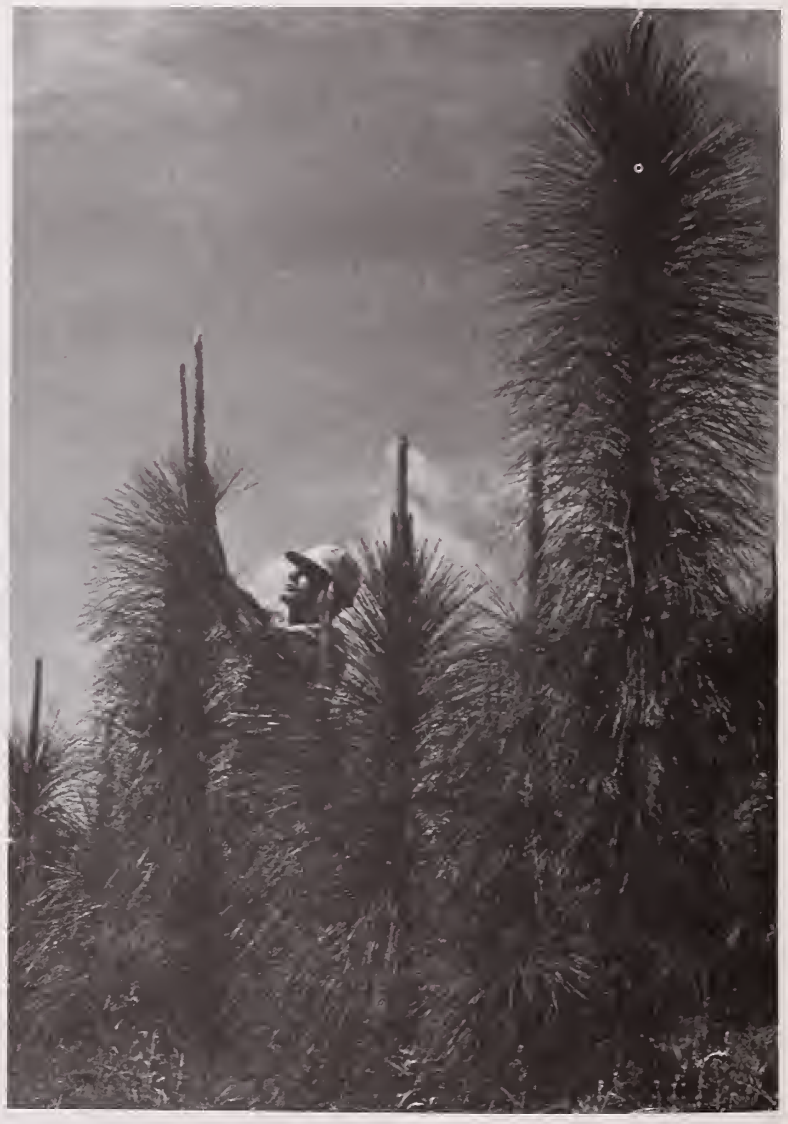

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Figure 3.—Intensively cultured longleaf pines at age 4 years.

to wider usage—poor planting success and delayed inception of height growth—can now be overcome. Intensive site preparation (fig. 3) promises further increases in the ease and reliability of artificial regeneration—prerequisites for the application of tree improvement.

The species is quite variable and therefore well suited for genetic manipulation. Available information indicates that significant genetic gains can be achieved in overall productivity as well as survival, early growth, and resistance to brown-spot needle blight. Research results are accumulating at a rapid rate, and much progress in practical tree improvement can be expected. This report reviews current knowledge on the genetics of longleaf pine and suggests improvement procedures.

SEXUAL REPRODUCTION

Reproductive Development

In natural stands, longleaf pines begin to produce cones and seed after attaining a diameter of at least 6 inches; that is, few cones are produced on trees less than 30 years old (Croker 1973). In intensively cultured plantations, however, cones have been observed as early as age 5 years.

Reproductive processes of longleaf pine resemble those of other southern pines and even of pines remotely related (Mohr 1896, Mathews 1932, Mergen and others 1963). Longleaf pine is monoecious, but occasional bisporangiate strobili are produced (Zobel and Goddard 1954). The timing of individual processes varies widely among years, locations, and individual trees. Unseasonably warm winters, for example, provoke early development; cool winters result in late but rapid development. Seasonal and locational differences generally parallel those in loblolly pine.

Male primordia are initiated in June, and female primordia are formed in July or August—about 27 months before seedfall (Eggler 1961). The first external evidence of male buds is an arching of branch tips in late September. Developing male buds appear as clusters of small knobs around bases of vegetative buds in early October on some trees but not until November or December on most trees. Female buds are first evident in October as asymmetrical swellings on vegetative buds and can be recognized individually in late November or early December. They are borne singly or in groups of two to six on primary or secondary branch tips. Details concerning the phenology of female reproductive development are given by Croker (1971b).

Pollen release and female receptivity occur in early February in Florida but not until mid-April near the northern end of the species range (Dorman and Barber 1956). Time of pollen release is related to heat sums above 10° C from January 1 onward (Boyer 1969, 1973, Boyer and Woods 1973). Longleaf pines generally are protandrous. Pollen shed usually is complete within a day or two in a particular tree but can occur over several weeks within a stand or seed orchard. Duration varies inversely with air temperature. In most trees, all female strobili become receptive within a few days of one another, but in some trees anthesis can extend over several weeks.

Cones ripen in October, approximately 18 months after pollination and 3 months after fertilization. Ripening generally occurs somewhat earlier in northern parts of the species range than in the south. Cone ripening in individual trees, nevertheless, is not related to time of female receptivity (McLemore and Derr 1965). Most seed in a given stand is shed within 2 weeks, but seedfall can extend over a month (Smith 1961).

Seed yields vary by year; yields average 60 seed per cone in good years, 35 in medium, and 15 in poor years (Wakeley 1954, Croker 1973). Within a given year, individual tree yields vary considerably.

Most mature trees produce some cones and seed each year. The incorrect impression of long intervals between crops results from the periodic occurrence of particularly large crops across the entire species range (Maki 1952). Because of losses to unfavorable weather and pests, numbers of recoverable cones are frequently far less than numbers of developing strobili. Heavy rains or freezing temperatures often interfere with wind pollination or reduce the number of developing cones. Insects also damage sizable numbers annually and can ruin entire crops (Allen and Coyne 1956). Reasonable forecasts of cone or seed yields can be made by assaying pollen abundance in the year preceding cone maturation (Boyer 1974), counting cones in March (Croker 1971a), or halving green cones longitudinally and counting exposed seed (McLemore 1962, Croker 1974).

Cross- and Self-Pollination

Normally, longleaf pine is a cross-pollinating species. Pollen is wind-disseminated. Male strobili usually occur in the lower crown and female strobili in the upper crown; sexes are mixed at mid-crown. Therefore, some selfing can occur, but its extent under natural and seed orchard conditions has not been quantified. A number of mutant alleles occur in natural populations (Snyder and others 1966), and some may be useful as genetic markers for studying the frequency of selfing.

Forms of inbreeding less drastic than selfing also occur, most likely as a result of past forestry practices. Isolated groups of trees remaining after logging were often the only source of seed for regeneration. Aberrant results from experiments involving isolated groups of trees have been attributed to such inbreeding (Snyder and Allen 1963).

Selfing and other forms of inbreeding reduce seed yields as well as survival and growth. Compared to cross-pollination, selfing reduced seed yields by 60 percent (Snyder and Squillace 1966), survival at age 8 years by 53 percent, and height growth by 33 percent (Schmitt 1968).

Controlled Pollination

Pollination techniques for longleaf pine are typical of those for other southern pines. In fact, the large strobili of longleaf pine were used to develop such techniques (Wakeley and Campbell 1954, Mergen and others 1955, Snyder 1957, Hesseltine and Snyder 1958, Snyder and Clausen 1974).

To obtain good pollen yields, male strobili should be picked as near maturity as possible. Strobili on a given tree are mature when some begin shedding pollen. However, delaying collection until maturity may often be impractical, and other, earlier signs of sufficient ripeness are described by Kraus and Hunt (1970). Pollen can be forced from late-maturing trees by bringing branches bearing male strobili indoors (Snyder 1961b) or by covering strobili on the tree with ventilated bags of clear plastic (Boyer 1969).

For extraction, strobili can be placed in viscose sausage casings or paper bags hung in a warm, dry room. Forced-air extractors have also been developed (Cumming and Righter 1948, Snyder 1961b, Summerville and Turner 1973, North Carolina State University 1974). Outdoors, pollen can be collected in viscose bags placed over ripening strobili.

Impurities, including insect larvae (*Cecidomyiidae* and *Xyelidae*) (Ebel 1963), can be removed from extracted pollen by straining through a 60-mesh sieve or voile cloth. Extraction equipment should be sterilized at 80° C for 12 to 15 hours, washed with alcohol, or exposed for several days to a sterilizing gas.

Freshly collected pollen should be dried until it pours smoothly or does not adhere to walls of glass containers. Vacuum desiccation is an efficient drying method (Snyder 1961b).

Although it is best to use pollen within several weeks of extraction, it can be stored for several years in small bottles only partially filled and stoppered loosely by cotton. A household refrigerator provides suitable conditions. Storage in air-tight containers at freezing temperatures has proven especially reliable (Callaham and Steinhoff 1966). A complete review of storage methods and conditions is given by Snyder and Clausen (1974).

Fresh pollen normally germinates well, but stored pollen should be tested for viability. Very dry pollen should be rehydrated before testing. A simple test for viability involves incubation for 72 hours in distilled water at room temperature and examination with a hand lens (Dillon and Zobel 1957). Only grains with a germination tube longer than the diameter of the grain should be counted as viable. Germination tube enlargement and test accuracy can be improved by incubation in a nutrient medium (Snyder 1961b).

Development of female strobili dictates when isolation bags should be put on, pollen applied, and bags removed. Campbell and Wakeley (1961) illustrate the developmental stages and provide guidelines for timing individual operations. In warm weather, progress of development must be checked daily.

Cone and seed yields from control-pollination usually are lower than those obtained from wind-pollination. Under good conditions, however, a skilled worker using proper care can achieve yields approaching wind-pollinated yields. In one year, Snyder and Squillace (1966), for example, reported yields equalling or exceeding those from wind-pollination. The opposite extreme also occurs; that is, seedless cones have been obtained from carefully planned and executed pollinations (Wakeley and Campbell 1960).

Seed Handling

To obtain maximum seed yields and germination, longleaf pine cones should be collected at maturity. Cones floating in 20-weight oil, i.e., with specific gravities of 0.89 or less, are considered mature (Wakeley 1954). Special precautions permit early collection (Barnett and McLemore 1970).

Longleaf pine seed are damaged easily during extraction and other processing operations. Adherence to prescribed procedures (USDA Forest Service 1974b), however, will provide seed with a germination rate approaching 100 percent as opposed to the usual 60 percent obtained via standard nursery practices. De-winging facilitates separation of full from empty seed but must be done gently because cracked seed deteriorates quickly (McLemore 1961b), especially in storage. Five methods are available for precise separation of sound and empty seed: weigh on a balance, drop on a metallic sounding board, determine if seed has a distinct "hila" (McLemore 1961a), float in pentane (McLemore 1965), and X-ray (Belcher 1973). The first three, however, require seed-by-seed examination. Seed with a moisture content of 8 to 10 percent and stored at 0° C will remain viable for 10 years or more (Barnett and McLemore 1970).

ASEXUAL REPRODUCTION

Longleaf pine is more difficult to propagate asexually than other southern pines. Cuttings can be rooted but not easily. Limited success has been obtained with air-layering, but grafting has proven reliable. Longleaf pine naturally reproduces by seed, although occasional seedlings sprout after damage or death of the main stem.

Rooting

Numerous methods of rooting cuttings, needle bundles, and air layers have been tested in attempts to preserve and multiply desirable genotypes. Early work indicates that cuttings from mature longleaf pine are as difficult to root as those from other southern pines (Dorman 1947, Johansen and Kraus 1958), and the approach remains impractical. More recent work with related species suggests that certain combinations of chemical treatment, environmental factors, branch girdling, and season of collection may greatly increase the percentage and consistency of rooting (Hare 1974, 1975). Needle bundles of longleaf pine can be rooted, but results are poor and few rooted bundles develop normally (Hare 1965, Wells and Raines 1965).

Air-layering has also been tried, but success varies inversely with ortet age (Johansen and Kraus 1958). In our repeated trials with young trees, the percentage of layers rooting in early summer was acceptable, but many treated branches broke before removal. Also, rooted air layers are difficult to establish and often exhibit topophysis.

Grafting

Grafting longleaf pine scions from mature trees onto seedling rootstocks is the most widely used method of establishing seed orchards. Cleft-grafting is the preferred method, but soft-tissue grafting is useful for propagating established clones (Zak 1955). Grafting success generally is less than that experienced with related species (Slade 1971). Hence, techniques used in other species (Vande Linde 1969) must be modified. Special precautions with regard to size of rootstock, timing of scion collection, and control of humidity and temperature in covering new grafts are necessary.

Commonly, grafts are made in early spring on 2-year-old rootstock grown in the nursery or in pots (Smith and Smith 1969). But grafted rootstock is difficult to transplant, and we have had better success with field-planted rootstock. Best results are obtained with vigorous rootstock having stems at least 6 inches long. Optimally, stems should be 18 to 30 inches long. From two to four growing seasons are needed to reach this stage of development.

Scion condition and timing of collection are important. In central Louisiana, for example, best success is achieved with dormant scions collected in mid-February. These are stored at 2° to 5° C and grafted about the third week of March, just as buds on rootstock seedlings begin to elongate. Methods for shipping loblolly and slash pine scions (Perry and Wang 1957a) can be used safely.

In longleaf pine, rootstock diameters normally exceed those of scions. Successful grafts can nevertheless be made as only one cambial layer must be aligned. We secure unions with grafting rubbers and also protect them with loose wrappings of aluminum foil. The foil reduces moisture loss and reflects solar radiation. Wrapped too tightly, however, the foil may restrict bud elongation. Further shading is not necessary, but irrigation is advisable.

In the event of graft failure, rootstocks normally develop another suitable shoot the following year. Also, several rootstocks can be planted together and grafted to further increase the probability of success.

Graft incompatibility has been experienced in longleaf pine (Goddard 1967). In our tests, about 14 percent of the ortets could not be grafted. As in other southern pines, however, graft incompatibility is more an inconvenience than an obstacle to seed orchard establishment.

Grafts between longleaf pine and certain other pine species or hybrids can be made, and some benefits have been reported. Open-pollinated seedlings of a natural slash × longleaf pine hybrid, for example, have been used as rootstock with good results (Gansel 1973).

VARIATION AND INHERITANCE

Longleaf pine is largely concentrated in the Atlantic and Gulf Coastal Plains but also extends into the Piedmont and Appalachian foothills (fig. 1). Elevations vary from sea level to 2,000 feet in northern Alabama. The frost-free period lasts 300 days in the south and 200 days in the north. Annual precipitation exceeds 50 inches over much of the range, and seldom is less than 40 inches. Rainfall is distributed rather uniformly throughout the year, but spring and summer droughts are common, especially in the western part of the range. Soils vary from deep, dry sands or low, wet sands near the coast to upland clays.

This diversity of environments has fostered development and maintenance of genetic variation among populations, or seed sources. In addition, local variations in soils and topography as well as annual variation in climate have caused considerable variation among individual trees within populations. Mutation, migration, and introgression have also contributed to variability within populations. Hence, the species contains much genetic variation among seed sources and individual trees.

Survival and Growth

Longleaf pine is plagued by poor survival and an extended grass stage. Advances in nursery and planting techniques (Brown 1964) and intensive cultural practices (Smith and others 1963, Mann 1969, Smith and Schmidtling 1970) are helping to alleviate these problems, but wide acceptance of the species will depend on improvements through selection and breeding.

Results from numerous provenance trials demonstrate extensive variation among seed sources in survival, duration of the grass stage, rapidity of early height growth, and volume productivity. Trees from coastal areas—partic-

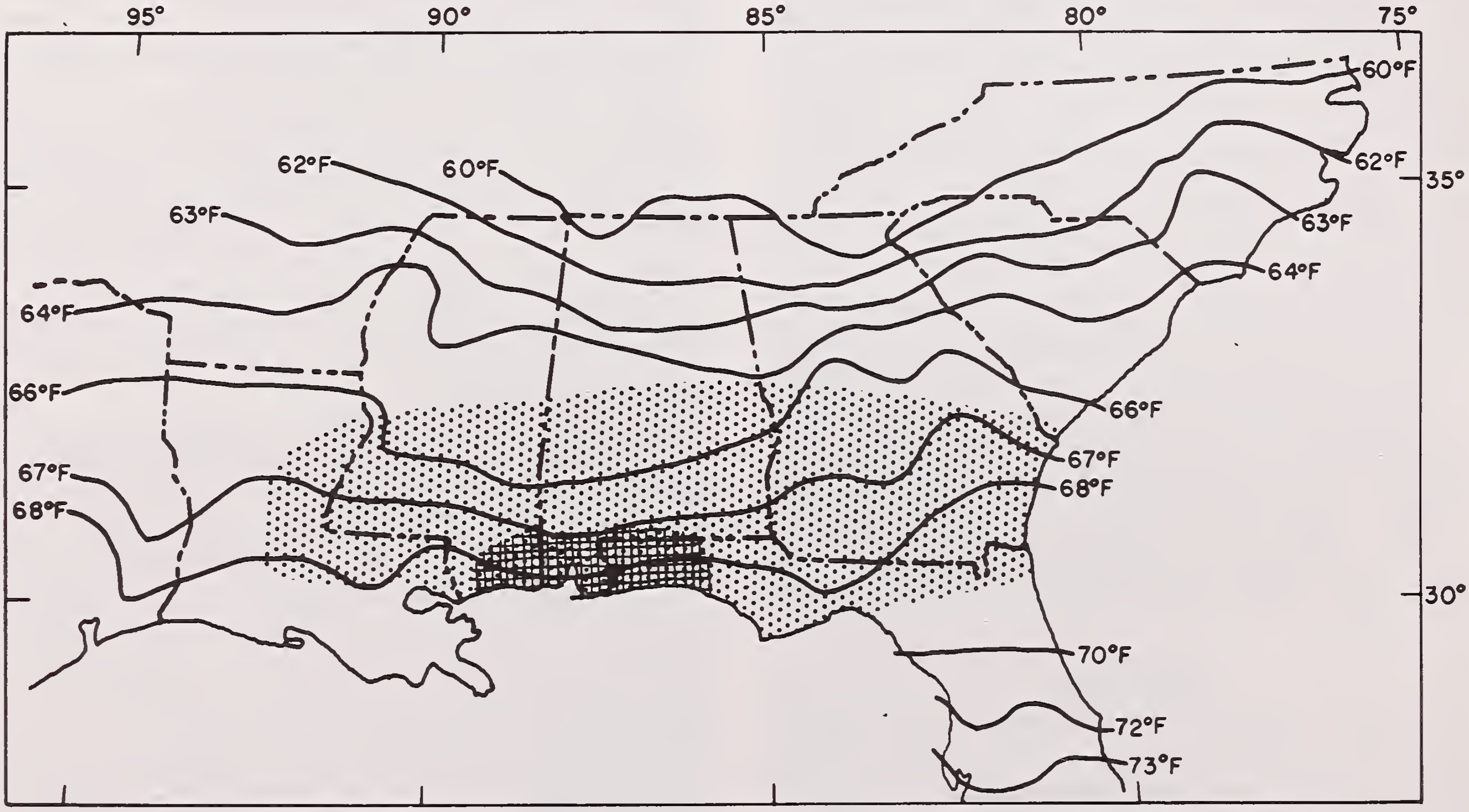

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Figure 4.—The Central Gulf Coast seed source (hatched area) and recommended planting zone (dotted area). (Adapted from Wells 1969.)

ularly the central Gulf Coast—generally outperformed those from inland sources at all but the coldest planting location (Wells and Wakeley 1970). Seed source × planting location interactions were generally absent. In at least six plantings, productivity of trees from Baldwin County, Ala., exceeded the average for each plantation by 58 percent or more. Thus, substantial improvement can be achieved by planting central Gulf Coast materials throughout much of the central portion of the range (fig. 4). The seed source should also prove valuable for selection of outstanding individual trees.

Other seed sources have merit for reforestation where central Gulf Coast materials have not performed well. Seed from Polk, Tyler, and Hardin Counties, Tex., seems desirable for use in western Louisiana and Texas (van Buijtenen 1965, Wells and Wakeley 1970). For the northeastern portion of the natural range, Wells and Wakeley (1970) recommend seed from near the border between North and South Carolina. Local sources should be used in the mountains of Alabama (Snyder and Allen 1968, Wells and Wakeley 1970). Until further information accumulates, local sources also seem best in Florida, except in the Panhandle where central Gulf Coast materials grow well. Trees from near Tampa, Fla., however, survive and grow poorly wherever planted (Allen 1961, Saucier and Taras 1966, Wells and Wakeley 1970).

Superiority of trees from the central Gulf Coast may be the result of adaptation to the warm temperatures and high rainfall (Shoulders 1965, Shoulders and Terry 1968, Wells and Wakeley 1970). Also, growth of most materials represented in the rangewide provenance tests of Wells and Wakeley (1970) was proportional to mean annual temperature at the origin of each seed collection.

Substantial variation in traits affecting survival and growth also occurs among individual trees. Survival is influenced by numerous environmental factors and therefore is difficult to measure with precision (Snyder 1973). Heritability estimates typically are low (table 1), but indirect selection appears promising. In an open-pollinated progeny test, Snyder (1973) achieved a 43-percent improvement in plot volume at age 15 years by selecting the tallest 10 percent of the families at 8 years. Increased productivity, however, was not so much a result of greater growth as of improved survival. Hence, selection for rapid early height growth indirectly improves survival. Similar results were obtained in our 13-tree diallel crossing experiment.[2]

A second indirect approach for improving survival involves selecting those families with the shortest terminal buds during the dormant season. Bud length was highly heritable in our 13-tree diallel crossing experiment (table 1), and the genetic correlation between dormant bud length and survival was −0.8.

Few tree species have as much phenotypic variation in early height growth as longleaf pine. Trees several years younger but many times taller than their associates are common (Pessin 1938). Mergen (1954) noted that numerous trees in an 18-year-old plantation had not begun height growth, but others were 38 feet tall. Such variability is diminished somewhat by intensive cultural practices (Schmidtling 1973). Substantial variability nevertheless persists on most sites, and a significant proportion is genetic, as demonstrated in progeny tests (fig. 5).

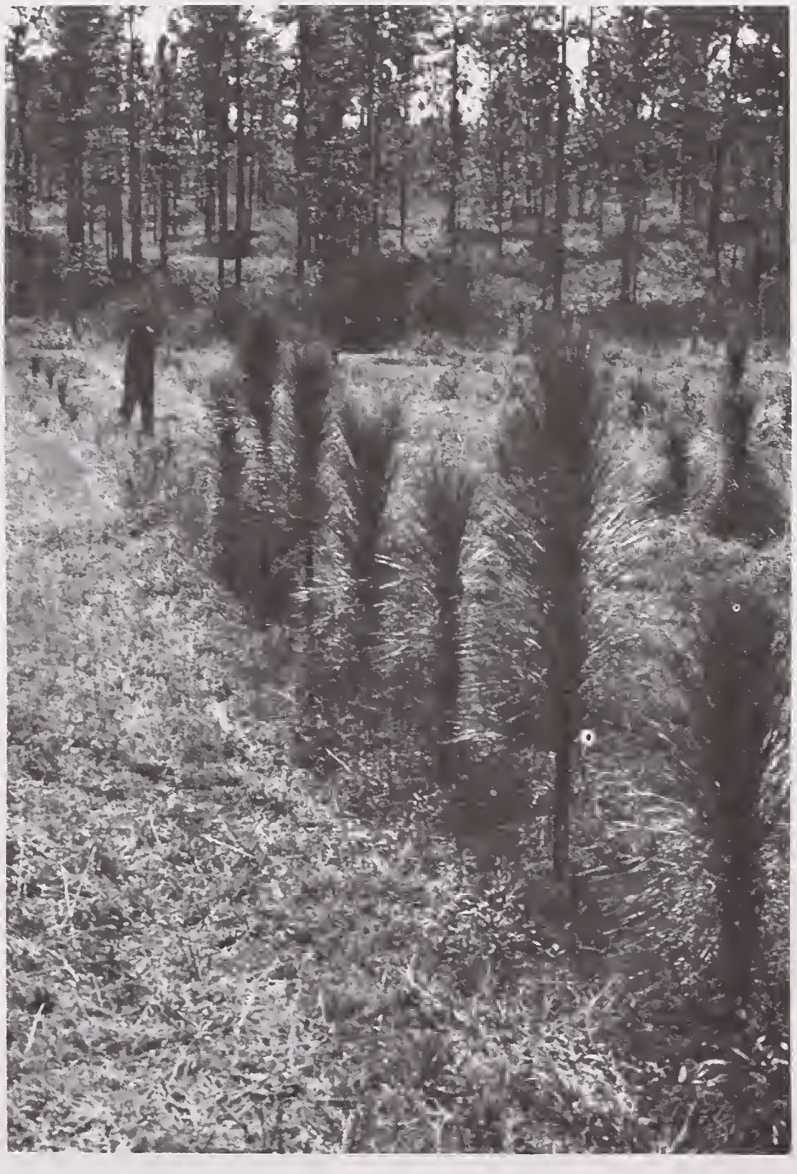

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Figure 5.—Some families like that in the foreground combine rapid early height growth and resistance to brown-spot needle blight.

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[2] Snyder, E. B., and Gene Namkoong. Inheritance in a diallel crossing experiment with longleaf pine. (in prep.).

Table 1.—*The heritabilities of longleaf pine characters*

Character	Heritability h^2
3-year height ($\overline{X} = 6.4$ in.), severe brown-spot needle blight	0.52[1]
3-year height ($\overline{X} = 23.6$ in.), brown-spot needle blight controlled	.48[2]
Brown-spot infection ($\overline{X} = 71$ percent)	.57[1]
Brown-spot infection ($\overline{X} = 55$ percent)	.30[1]
5-year survival	.09[3,4]
5-year height	.12[3]
8-year height	.53[3]
8-year height (parent-progeny)	.48[3]
β-pinene percentage	.30[5]
β-pinene percentage (parent-progeny)	.60[5]
3-year height	.16
5-year height	.18
7-year height	.12
7-year height (parent-progeny)	.43
7-year basal area	.12
7-year form class	.06
7-year volume	.07
7-year survival	.03
7-year-volume (plot)	.03
Forking percentage	.06
Fusiform rust infection percentage	.12
Branch angle (at attachment)	.29
Branch angle (average)[6]	.43
Branch length	.19
Branch length/bole height	.17
Knot area/basal area	.07
Branches (number)	.21
Branch volume/bole volume	.22
Percentage of stem covered with needles	.42
Percentage of branch covered with needles	.16
Needle droop angle	.29
Needle circumference	.26
Weight/needle	.36
Needle length	.34
Needles/tree (number)	.15
Foliage green weight	.11
Foliage green weight adjusted by bole volume	.10
Foliage surface adjusted by bole volume	.08
Dorsal stomates within row (number)	.39
Rows of dorsal stomates (number)	.47
Total dorsal stomates (number)	.56
Bud scale width	.12
Bud scale length adjusted by width	.14
Bud diameter	.27
January bud length	.62

[1] Test of 540 wind-pollinated families (Snyder and Derr 1972).

[2] Test of 490 wind-pollinated families (Snyder and Derr 1972).

[3] Test of 100 wind-pollinated families (Snyder 1969).

[4] This and similar types of traits in this table based on plot means; four times the additive variance has been used as the numerator in the h^2 formula.

[5] Test of 13 diallel-crossed parents (Snyder and Namkoong, manuscript in preparation). The remaining values of this table are from this source.

[6] Angle formed between the stem axis and a line extending from the stem to the branch tip.

In a large open-pollinated test of random parent trees, overall average height at age 8 years was 6 feet, but averages for the best 20 families ranged from 7 to 10 feet and the poorest family averaged only 1 foot (Snyder 1969). The best 25 percent of the families as judged on the basis of parental phenotypes were 12 percent taller than the plantation average. Selection of a similar proportion on the basis of progeny test results, however, yields a 35 percent increase—a 23 percentage point advantage over phenotypic selection. Hence, progeny testing appears almost three times more effective than phenotypic selection—an outcome expected in view of the early growth pattern of longleaf pine. Moreover, the most exceptional parents would probably have gone undetected in the absence of progeny testing, as they were not phenotypically exceptional (fig. 6).

The advantages of early progeny testing persisted through age 15 years (Snyder 1973). In spite of decreased variation in height, the families that grew fastest at early ages produced the most wood per unit area in later years. Improved diameter growth and especially improved survival accounted for their superiority.

Efforts to improve early survival and growth would benefit from knowledge concerning the physiological basis of the grass stage; attempts to modify this growth habit by physiological manipulation have thus far failed. Allen (1958) and Brown (1964) examined growth substances in grass-stage seedlings. Apparently, such seedlings have the potential for producing growth-stimulating auxins, but mechanisms for transport are absent or perhaps blocked by inhibitors. Future research on the physiological basis of the grass stage will be aided by availability of fast-growing material from progeny tests.

Resistance to Pests and Environmental Stress

Brown-spot needle blight, caused by *S. acicola,* partially or completely defoliates seedlings. Progressive defoliation in successive growing seasons prolongs the grass stage and, if not controlled, can cause death. Surviving but chronically diseased seedlings often remain stunted or grow slowly (Wakeley 1970, Boyer 1972). The disease occurs throughout the species range but is a chronic problem only in the Coastal Plain west of Panama City, Fla. (Wakeley 1954).

Infestations can be controlled with fungicides or prescribed burning (Lightle 1969). However, control with fungicides is economical only in nurseries, and prescribed burning can damage healthy seedlings in the early stages of height growth. A more promising solution is the development of resistant strains through genetics research.

Genetic variation in resistance is extensive among seed sources. Seedlings from north Alabama, for example, often remain disease-free when planted locally but are quite susceptible when grown near the Gulf Coast (Snyder and Allen 1968). In contrast, seedlings from the central Gulf Coast, which excel in survival and growth, have also proven resistant at a variety of locations (Bethune and Roth 1960, Henry and Wells 1967, Derr 1971, Snyder and Derr 1972). Materials from west of the central Gulf Coast seed source (fig. 4) generally are susceptible, but those from east of that area perform unpredictably.

Striking variation in resistance also occurs among individual trees. Disease-free seedlings have long been observed in infected areas. One resistant phenotype from a heavily infected nursery consistently has yielded wind- and control-pollinated seedlings with substantial resistance (Derr 1963, Derr and Melder 1970). In an open-pollinated test involving 227 plus-trees from seven States, percentages of resistant seedlings per family ranged from 2 to 89 (Derr 1971). In a similar test of 540 parents, percentages of diseased needle tissue averaged 48 for the best 54 families and 63 for the general population (Snyder and Derr 1972). Heritability estimates were moderate to high (table 1). Comparisons between protected and unprotected plots indicated that rapid early growth was one, but not the only, mechanism of resistance. High resin content has also been suggested as a factor in resistance (Verrall 1934).

Previous progeny tests provide guidelines for selecting and testing seed orchard candidates (Snyder and Derr 1972). Prospective parents should be selected from previously damaged plantations, nurseries, and natural stands since such materials proved more resistant than those derived from areas where infection was light or unknown. Progeny tests should be conducted on sites where natural infection is severe. Establishment of susceptible spreader seedlings and clean cultivation also serve to intensify disease. Under such conditions, accurate evaluations of resistance and early growth can be had within 2 to 4 years of planting. A system for artificially inoculating seedlings is being developed at the Southern Forest Experiment Station.

Resistance to fusiform rust (*C. fusiforme*) is common in longleaf, but some variation has been found among seed sources and individual trees. Trees from Alabama and Georgia sources

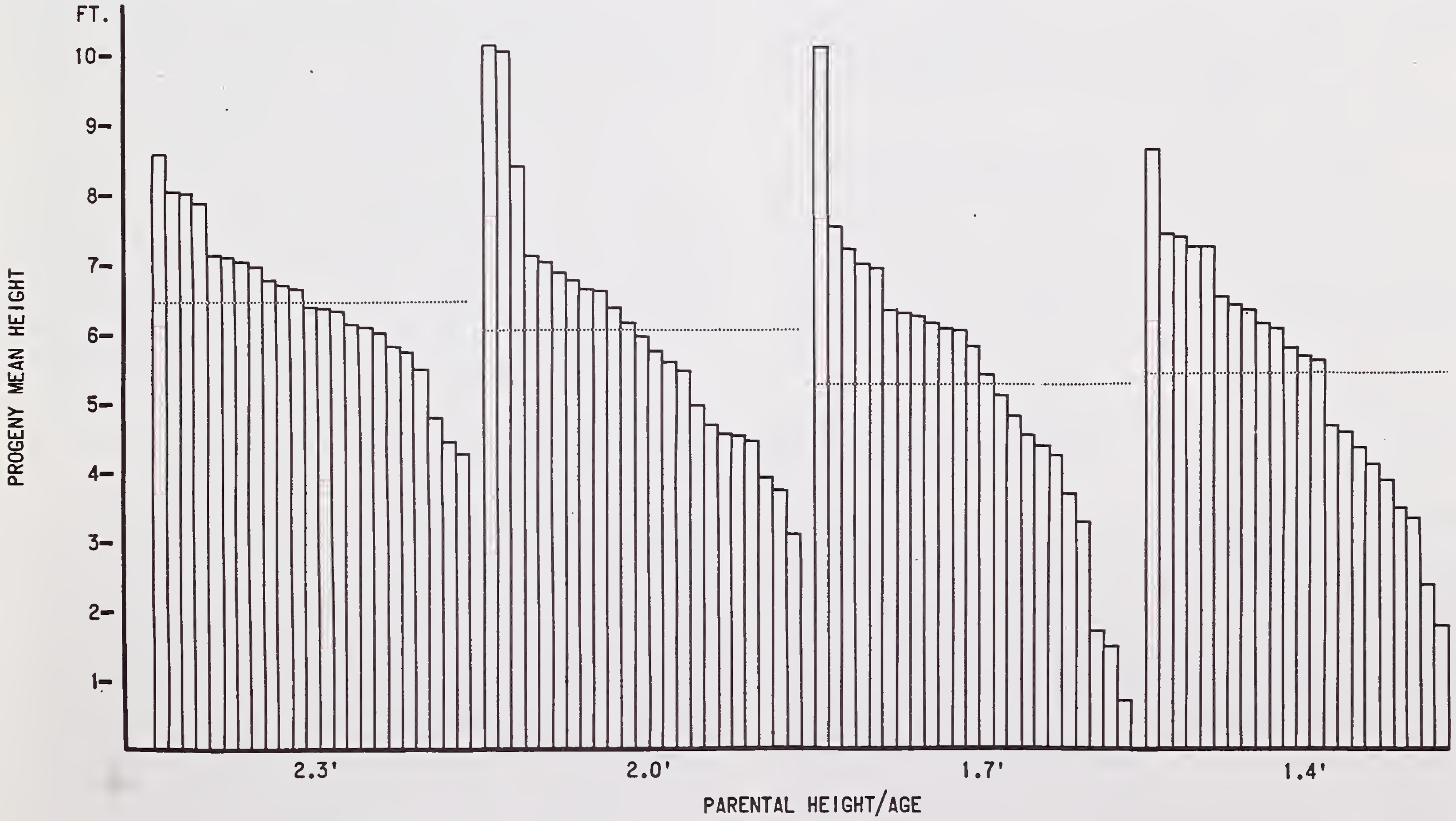

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Figure 6.—Mean 8-year heights of open-pollinated progenies from 91 random parent trees. The four groups represent quartile ranking of parents on the basis of phenotype (parental height: age ratios). Group means are indicated by dotted lines. On the average, progeny means are based on 28 trees.

proved less resistant than those from Louisiana or Texas in the Southwide Pine Seed Source Study (Wells and Wakeley 1970), and infection rates as high as 64 percent have been observed in progeny tests. Hence, breeders must take care lest they bring together susceptible trees. A simple roguing of seed orchards on the basis of progeny tests seems sufficient.

The occasionally high incidence of rust has led to concern that rust susceptibility is correlated with brown-spot resistance and rapid early growth. Such relationships have been noted (Wakeley 1968), but our observations of numerous progeny tests do not confirm a relationship with brown-spot resistance. We, however, found positive genetic correlations between rust susceptibility and certain growth traits. Such correlations may be a result of introgression with loblolly pine; for example, we also found negative correlations of rust susceptibility with bud and branch diameters—evidence of introgression.

Resistance to cold and ice can be critical to planting success. Longleaf pine is not particularly frost hardy (Parker 1959, 1965) but resists ice damage as well as or better than related species (McKellar 1942, Cool and others 1971, Van Lear and Saucier 1973). Northward movement of seed, however, can result in impaired growth and form. Seedlings from a Tampa, Fla., seed source, for example, suffered considerable frost damage when grown in Virginia (Allen 1961).

Form and Crown Characteristics

Longleaf pine as a species is highly regarded for its straightness. Crookedness is encountered occasionally but may be caused by environmental factors. Little information is available concerning inheritance of straightness in longleaf pine, but work in other southern pines indicates that this important trait is under strong genetic control. Little variation in taper was found among families in our 13-tree diallel crossing experiment.

Natural longleaf pine stands typically contain few trees with bilateral or ramiform forks. Yet, forking occurs with alarming frequency in young, fast-growing offspring of straight, well-formed parents (Stephenson and Snyder 1969); fortunately, heritability is quite low (table 1). Provenance tests also suggest an association with growth rate. Collins (1964) found that trees from his best seed source, Baldwin County, Ala., had the highest incidence of forking. In many cases, however, forking is probably caused by insect damage to terminal buds. Young trees frequently overcome the defect and survive as single-stemmed, reasonably straight trees. Large knots are the most serious outcome.

In sum, longleaf pines with desirable stem form are common, and variability in contributing traits seems small or lacking. Until more information becomes available, emphasis in selection and breeding is best directed toward traits having more direct effects on yield.

Longleaf pine generally prunes well in adequately stocked stands. Yields of clear lumber are high but less than those from slash pines of similar age and diameter. Knots are fewer but larger in longleaf pines than in slash. Snyder (1961a) suggested that pruning ability varies directly with branch angle. Knot size, on the other hand, varies indirectly with branch angle. Individual trees vary greatly in branch angle, and significant improvement seems possible since the trait is under moderate genetic control (table 1). Heritabilities for other branch and foliage traits affecting the quality and quantity of timber produced are given in table 1. There are two major problems in breeding for branch traits. Branch length and number are correlated with volume; hence, improvement in volume may cause parallel increases in branch numbers and length—a situation opposite that sought in crown efficiency schemes (Boyer 1968, Strickland 1968). Also, conditions in natural stands tend to obscure genetic differences in branch traits; so selection of parent trees is complicated.

Wood Properties and Naval Stores

Longleaf pines almost always have higher stemwood specific gravities and produce more dry wood per unit volume than loblolly or slash pines (Zobel and others 1972). Available data on geographic variation in wood properties of longleaf pine indicate an association of specific gravity with climate and physiography (Mitchell 1964, USDA Forest Service 1965, Saucier and Taras 1969, Wahlgren and Schumann 1972, Zobel and others 1972). Generally, trees in areas with abundant summer rainfall and warm temperatures have higher specific gravities than those in drier areas or colder climates. Hence, wood density decreases from south to north across the Coastal Plain into the Piedmont. Similar patterns often occur even within States. In Mississippi, for example, specific gravity decreases from southeast to northwest along the natural gradient of decreasing summer rainfall (Mitchell 1962). In North Carolina, however, differences in specific gravity, extractive content, and moisture content were smaller among counties than among individual trees within counties (Quijada 1967).

When trees from different seed sources are grown at common locations, these patterns of natural variation do not necessarily persist. The few provenance tests analyzed to date have revealed no meaningful genetic differences among seed sources in specific gravity (Strickland 1965, Saucier and Taras 1966). Results from progeny tests nevertheless suggest that genetic variability among individual trees in the most important wood properties will be on a par with that in other southern pines.

Longleaf pine is second only to slash pine in the quantity and quality of naval stores it produces (Dorman in press). The oleoresin crystallizes less rapidly and the oils volatilize more readily than those of most other southern pines (Herty and Dickson 1908), probably because of fewer components (Mirov 1961). The volatile fraction, for example, consists primarily of alpha- and beta-pinene. In general, composition varies only slightly among seed sources, but large differences have been observed among individual trees. Over half the total genetic variance and slightly less than half the phenotypic variance in beta-pinene content was additive (Franklin and Snyder 1971). Considerable genetic variation among yields from individual trees has also been reported (Mergen 1953). Both yield and composition can therefore be manipulated genetically, and an improvement program has been initiated at the Southeastern Forest Experiment Station.

Mutant Forms

Mutant forms with abnormal hypocotyl and primary needle coloration as well as various morphological abnormalities have been reported. Some may prove useful as genetic markers, but inheritance patterns of even the most obvious and frequent have not been quantified.

Our examination of 12,359 seedlings from 142 half-sib families germinated in the laboratory indicated that alleles for abnormal hypocotyl pigmentation occurred in 7 percent of the families as compared to 19 percent found in slash pine by Snyder and others (1966). In a separate nursery experiment, we found similar forms in 10 of 572 longleaf families. One albino type was recovered from a cross between longleaf and shortleaf pines (Campbell and others 1969). Workers at the Southeastern Forest Experiment Station observed seedlings with yellow primary needles in a provenance test but found no recognizable geographic pattern.

Morphological abnormalities are found in practically every phase of growth and development. Ferré (1958) observed a seedling completely lacking cotyledons. Stephenson and Snyder (1969) observed trees without branches—foxtail forms—and trees retaining stem needles long after leaving the grass stage (fig. 7). Occasional forms with dichotomous branching have been noted, and a weeping strain with 24-inch needles has been reported (Coker and Totten 1934). Most male strobili are bluish during development, but a small percentage of trees have yellowish or other colored strobili. Significant numbers of trees produce seed with loose or easily removed wings, a trait possibly of direct value in tree improvement.

In attempts to induce mutations, longleaf pine seed proved less sensitive and seedlings more sensitive than those of slash pine to low levels of X- or gamma-radiation (Snyder and others 1961, Davis 1962, McCormick and McJunkin 1965). At higher radiation levels, however, longleaf pine seed failed to germinate (Davis 1962).

INTERSPECIFIC HYBRIDIZATION

The major southern pines and certain minor species are closely related and have overlapping ranges. Natural hybridization therefore contributes to genetic variation among populations, stands, and individual trees. Interspecific hybrids of longleaf pine, both natural and artificial, are being examined as means for obtaining disease resistance or other desirable traits from closely related species.

The success of species hybridization has been predicted on the basis of similarities in cotyledon morphology (Ferré 1965). In general, such predictions—*P. palustris* × *P. serotina* = impossible, × *P. echinata* = very difficult, × *P. taeda* = difficult, and × *P. elliottii* = easy—have agreed with results from control-pollinations (Snyder and Squillace 1966). There are no confirmed reports of successful crosses with other species in Subsection *Australes.* Also, in the opinion of Ferré (1965), viable hybrid seeds will not be obtained from crosses of longleaf pine with species in other sections of the genus.

Cone and seed yields from pollinations to produce F_1 species hybrids generally are lower than those from pollinations within the species (Snyder and Squillace 1966). Hence, practical

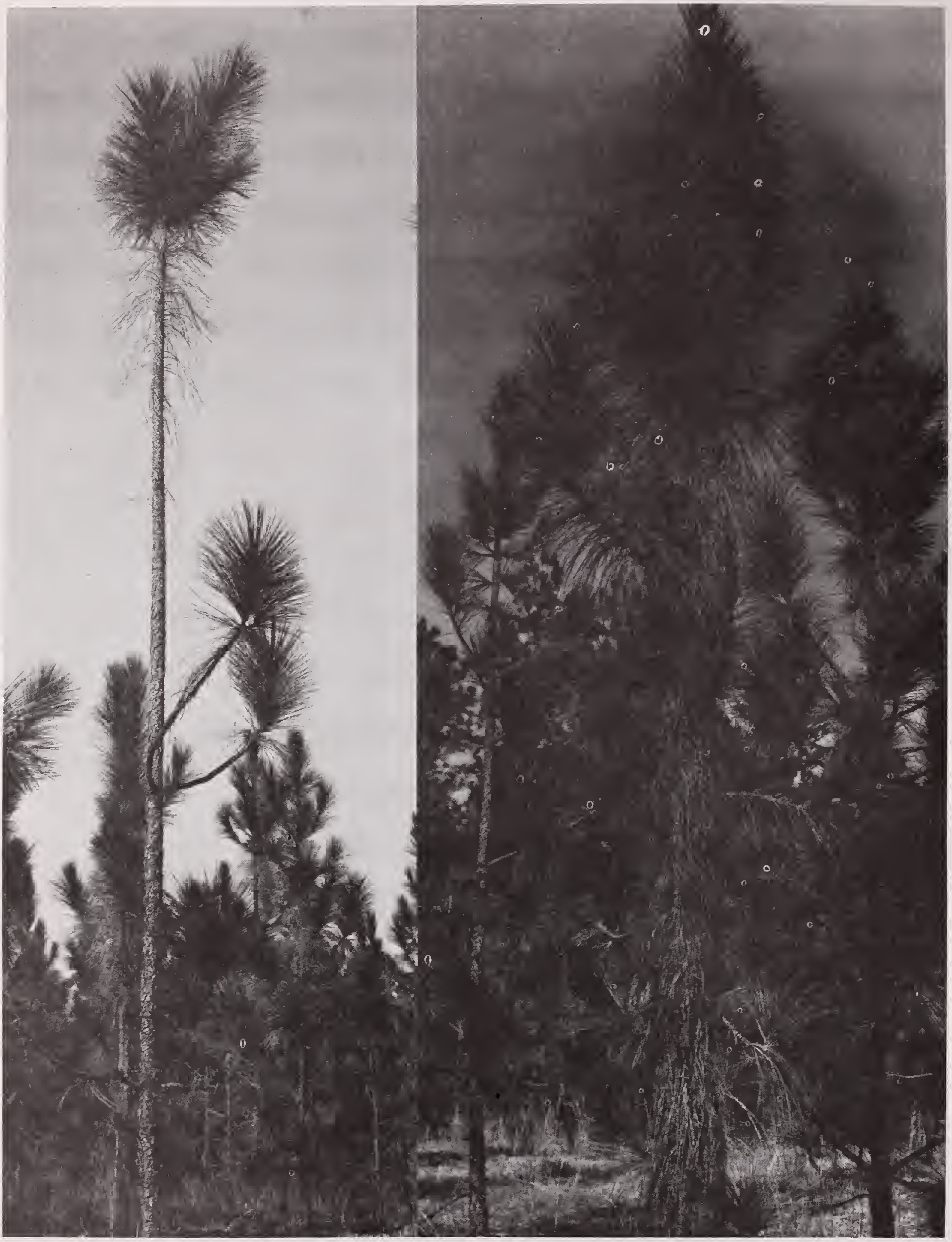

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Figure 7.—Two mutant forms: a nearly branchless foxtail (left) and a tree with persistent stem needles (right).

application of hybrids is limited by difficulties with seed production. Seed yields from crosses between two particular species vary widely depending on individual parents (Critchfield 1963). Selection of compatible parents therefore provides one means of increasing yields.

Longleaf × Loblolly Pine Hybrids

Sonderegger pine (*P.* × *sondereggeri* H. H. Chapm.), the hybrid between longleaf and loblolly pines, was the first recognized and is the only named southern pine hybrid. Natural hybrids are common, especially in areas along fringes of the longleaf pine range. Longleaf pine seedlots frequently contain hybrid seed in amounts of less than 1 percent, but collections containing as much as 33 percent have been reported (Wells and Wakeley 1970).

Sonderegger pines established early in this century have characteristics intermediate between those of the parent species (Namkoong 1966). Such hybrids probably originated from F_1 crosses involving the few longleaf pines left after logging. Recent hybrid forms, on the other hand, are the result of extensive backcrossing with longleaf pines. Hence, Sonderegger pine, as presently viewed, comprises a complex of F_1 and F_2 hybrids as well as various backcross derivatives. As a further result, most present-day longleaf pines are thought to contain some loblolly pine genes.

Hybrid forms are readily discernible in longleaf pine nursery beds because of conspicuous height growth (Sherry 1947). Most morphological characteristics at the seedling (fig. 8) and later ages are nevertheless extremely variable. Also, wind-pollinated offspring from one hybrid resembled not merely longleaf and loblolly pines but also slash pine (Schmidtling and Scarbrough 1968). Seed weight and bud or adjacent branch diameters are excellent indicators of hybridity as their ranges seldom overlap those of the parent species. Some cone traits are useful (Namkoong 1966). We also observed that prickles on hybrid cones point outward like those of loblolly pine but are longer and sharper than those of either parent species. Most needle traits generally are intermediate to those of parents (Keng and Little 1961), but needle lengths and widths resemble those of loblolly more than longleaf pine (Namkoong 1966).

Forestry application of Sonderegger pine or its derivatives has received wide attention. Chapman suggested breeding the hybrid in 1922—an early recommendation for improving pines. Improvement will nevertheless be difficult as most Sonderegger pines survive poorly, grow slowly, have poor form, and are susceptible to pests (Wakeley 1927, Allen and Coyne 1956, Hoekstra 1957, Kraus 1963, Dorman 1966, Schmitt 1968, Grigsby 1969, van Buijtenen 1969).

Further effort seems justified, however, as the complex is highly variable, and we have observed hybrid and backcross progenies with desirable combinations of traits. Hybrid forms sometimes outperform longleaf pine (Wells and Wakeley 1970) and even loblolly pine (Schmitt 1968, Schoenike and others 1975). Conceivably, repeated backcrossing to selected longleaf pines, accompanied by selection each generation for growth, will yield a derivative with the desirable attributes of longleaf pine and the rapid early growth of the nonrecurrent loblolly pine parent. Fusiform rust susceptibility, for example, can be minimized in a single generation of backcrossing. Finally, hybrid forms are prolific seed producers, and reproductive events are synchronized with those of the parent species—advantages not offered by most species hybrids.

Longleaf × Slash Pine Hybrids

Natural longleaf × slash pine hybrids occur infrequently except in southern Georgia and northern Florida, where reproductive events commonly coincide (Perry and Wang 1957b). Artificial hybrids are produced with relative ease; for example, Derr (1966) obtained significant numbers simply by dusting slash pine pollen on exposed female strobili of longleaf pine.

Seedling hybrids are identified easily as they lack the grass stage typical of longleaf pine (Mergen 1954, Harkin 1957). Several traits are useful for identifying older hybrids; we found the intermediate sheath length of 1-year-old needles the best indication of hybridity. Hybrids resembled longleaf more than slash pine in needle length and percentage of fasicles with three needles. Numbers of stomates per mm of needle length were intermediate between longleaf and slash but more variable than those of either parent species (Mergen 1958). Chromosomal irregularities are more common than in either parent species (Saylor 1967). Differences between hybrids and their parents are accentuated on poor sites.

Longleaf × slash pine hybrids show promise on dry, sandy sites. Under such conditions, height growth begins earlier than that of longleaf, and growth in later years exceeds that of slash pine (Mergen 1954). Rapid early growth generally minimizes the effects of brown-spot needle blight in plantations. Individual hybrid progenies with excellent growth and form, as well as resistance to fusiform rust and brown-spot needle blight, have been noted (Kraus 1963, Derr 1966, Schmitt 1968, Long 1973). Most traits are affected by individual longleaf and slash pine parents (Derr 1966, Schmitt 1968), and hybrids between carefully selected

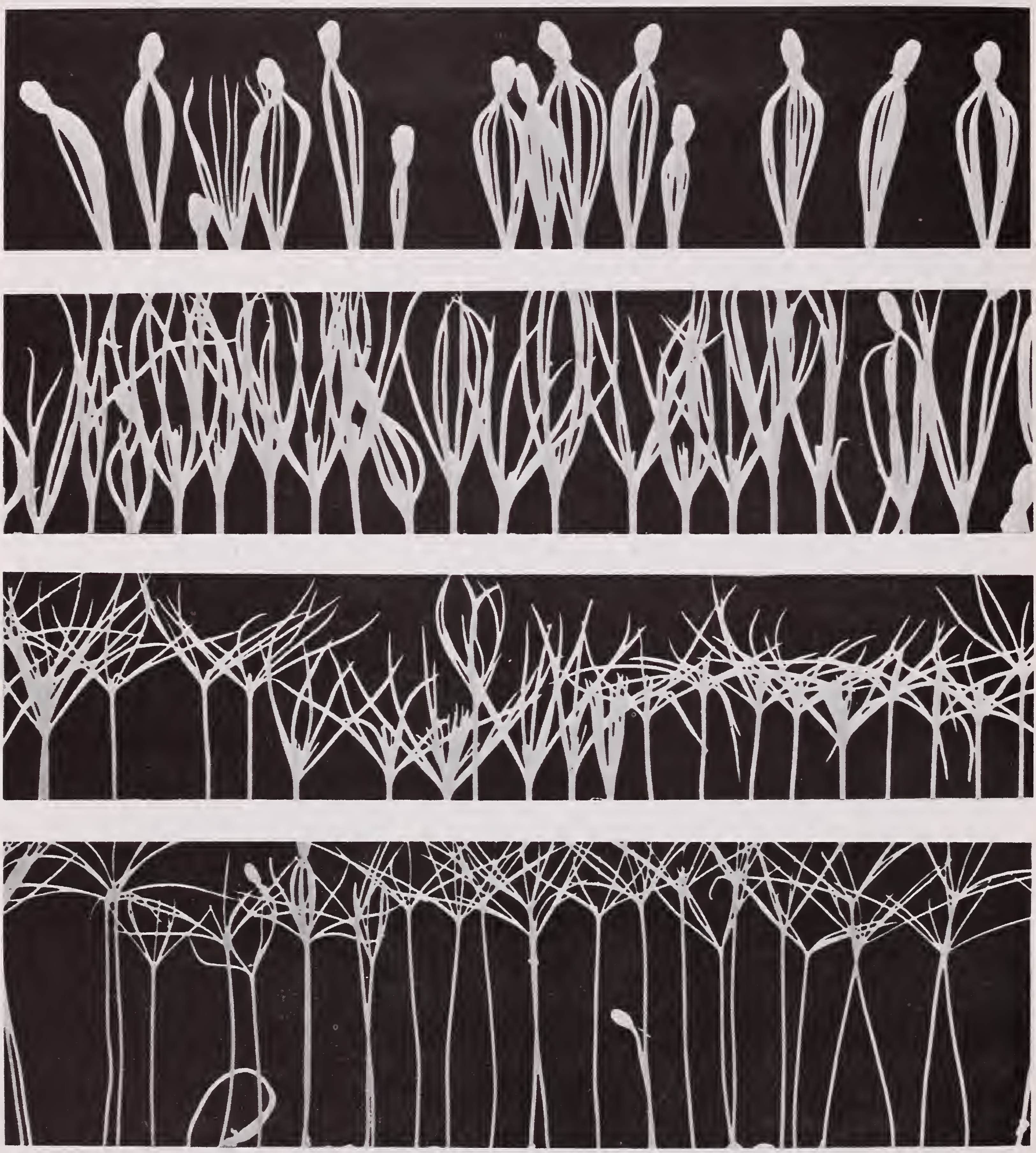

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Figure 8.—Crossing longleaf and loblolly pines generates extensive variability in hypocotyl length. Top row, longleaf pine; second row, F_1, Sonderegger pine; third row, F_2 progenies; fourth row, loblolly pine. (Adapted from Brown 1964.)

parents should be quite useful. Backcrosses and other derivatives are also being tested (Goddard and others 1963).

Longleaf × Shortleaf Pine Hybrids

Hybrids between longleaf and shortleaf pines have not been reported in nature but have been produced artificially (Snyder and Squillace 1966, Campbell and others 1969). The cross is effected with difficulty, and the hybrid therefore is mainly of scientific interest. Of 20 traits examined by Campbell and others (1969), 14 tended to be intermediate relative to the parental species. Morphological features of strobili provided the clearest evidence of hybridity.

IMPROVEMENT PROGRAMS

Tree improvement efforts in longleaf pine are less advanced than those in other major southern pines. A 1971 listing indicated only 245 acres of established longleaf pine seed orchards (USDA Forest Service 1971). Few orchards were producing commercially important quantities of seed, and the area represented only a fraction of that established for loblolly and slash pine. A more recent survey (USDA Forest Service 1974a) indicates a 34 percent increase in the area of longleaf pine orchards. The current figure of 329 acres is still far below that for loblolly and slash pines, but the appreciable increase signals renewed emphasis on the selection and breeding of longleaf pine. Plantable seedlings are now being produced from 52 percent of the established orchard areas. Though the increased interest is encouraging, improvement of the species merits even greater emphasis.

Procedures

In terms of most economically important traits, longleaf pines contain as much or more genetic variation than other southern pines. Seed source variation is such that separate seed orchards are required for planting specific areas or growing particular end products. Useful guides for seed collection and movement have been formulated (Wells 1969). The central Gulf Coast seed source, for example, is noted for its superior growth and brown-spot resistance, and seed from this area is recommended for planting in east central Louisiana, southern Mississippi, Alabama, and Georgia, and north Florida (fig. 4). Recommended seed collection and planting zones may change as existing or new provenance tests mature.

Variation among individual trees within a particular portion of the range exceeds that among seed sources, and improvement efforts based on individual tree variation are well justified. Selection of the best individuals from the recommended seed sources will provide added improvement. However, large numbers of trees should not be selected from any one stand because many modern stands, especially in Louisiana and Texas, developed from the few trees left after logging or farming and inbreeding could become a problem.

The typical procedure of placing phenotypically superior parent trees directly in clonal seed orchards is not suited for longleaf pine. Because of the grass stage and brown-spot infection, a longleaf pine may appear to be several years younger than it actually is. Also, the extreme variability in survival and early growth within a natural stand results in uneven competition that may mask inherent potential for growth and other desirable traits influenced by stand density. Progeny testing therefore is essential for improving survival, early growth, and brown-spot resistance.

Much evidence has accumulated concerning the effectiveness of short-term progeny testing before seed orchard establishment. For example, the best 25 parent trees selected from a sample of 100 on the basis of performance by wind-pollinated progeny yielded materials 35 percent taller than the population average at age 8 years (Snyder 1969). In contrast, offspring from the 25 parent trees chosen solely on the basis of phenotypic appearance were only 12 percent taller. The truly outstanding parents—the best 3 percent—were not among those obtained by phenotypic selection with or without the use of comparison trees. In the same experiment, gains in plot volume at age 15 years were 43 percent from progeny testing and 15 percent from phenotypic selection alone (Snyder 1973). Much of the difference resulted from increased survival and early growth.

In a similar experiment, Goddard and others (1973) noted that progenies from trees of generally good quality performed as well as those from rigorously selected plus-trees. In view of such findings, the University of Florida Cooperative Tree Improvement Program has shifted emphasis from phenotypic selection alone to a less stringent form of selection and short-term progeny testing. Large numbers of well-formed dominant trees are selected for evaluation, and only those whose progenies perform well will be grafted into seed orchards.

Indications are that the most valuable parent trees can be identified within 5 years of progeny test establishment. Reliable results as well as considerable savings in time and money are obtained by testing wind-pollinated materials (Schoenike and Williams 1975). In our 13-tree diallel crossing experiment, general combining abilities derived from wind-pollinated materials corresponded closely to those from control-pollinated materials.

In addition to identifying the best parents for grafting into clonal orchards, the progeny tests themselves can be rogued for conversion to low-cost seedling seed orchards. Seedling orchards have particular merit in longleaf pine, especially in programs stressing resistance to brown-spot needle blight. Seedlings can be planted at close spacings in areas of high disease incidence and evaluated periodically for resistance, survival, and early growth. Susceptible materials not killed by the disease can be rogued, leaving only the best trees in the most resistant families. Also, the best of the released individuals can serve as sources of material for an early start on advanced generation breeding.

Procedures typically employed in improving other southern pines have been applied to longleaf. Phenotypically superior trees have been selected from the general population and established in clonal orchards, and information from subsequently established progeny tests is being used to rogue and upgrade the breeding population. Such procedures will result in some improvement but are less efficient than progeny testing before seed orchard establishment since they do not fully adjust for important differences between longleaf pine and its associates.

Regardless of the procedures chosen, agencies interested in establishing clonal or seedling seed orchards should concentrate their efforts on those economically important traits under moderate to strong genetic control. For most important traits, a significant proportion of the genetic variability observed in progeny tests is additive (table 1), and rapid progress in improvement is anticipated. Gains will be greatest for traits with strong parent-progeny correlations. For many growth traits, heritability estimates obtained from parent-progeny relationships correspond to those based on progeny performance alone. Several important traits—survival, rust resistance, diameter, volume, and branch length—are not inherited strongly but are correlated with other traits and can be improved by indirect selection. The necessary phenotypic and genetic correlations are often calculated along with heritability estimates and can be obtained from the papers listed in table 1.

Some genetic variation among individual trees is nonadditive. Specific combining ability effects—a measure of such variation—were apparent for almost half of the 51 traits examined in our 13-tree diallel crossing experiment. Such effects, however, were small relative to total phenotypic variation, and breeding programs employing nonadditive variation appear impractical, at least until the larger and more easily obtained gains from additive variation have been exploited.

Different approaches to improvement are also being considered. Breeding methods involving selfing, species hybridization, haploid induction, polyploidy, and mutagenesis are either practiced on a small scale or in the experimental stage. Selfing and hybridization have been employed to produce special purpose strains, but success is limited by generally poor seed yields. Production of homozygous diploids in tissue culture would be a welcome substitute for selfing because of the shortened generation time (Brown 1967).

Seed Orchards

Returns on investment in tree improvement depend upon seed orchard productivity. Some estimates suggest, however, that longleaf pine seed orchards will produce 25 percent less seed than slash pine orchards of comparable size (Chapman 1971). Special care in orchard location, protection, and management is therefore of critical import.

Fertile, well-drained sites readily accessible and easily protected against pests are a prime requirement. Should yields prove less than in other species, other locations should be considered in areas inside or outside the species range where the environment fosters seed production. Provenance tests, for example, indicate that seedling materials produce cones earlier and bear larger crops when moved southward (Boyer and Evans 1967). This single observation may indicate only a temporary precocity, but the potential should not be overlooked. Perhaps annual seed yields over a period of years could be summarized by locality and the results used to evaluate areas for orchard establishment. Observations of progeny and provenance tests could likewise be employed. Orchards established outside the area of intended usage, however, should be so located as to avoid pollination by undesirable sources (Boyer 1966).

Experience with longleaf and related pines clearly indicates that protection against insects and disease is necessary to insure productivity. *Dioryctria, Laspeyresia, Tetrya,* and *Leptoglossus* species frequently destroy as much as 70 percent of the potential cone and seed crop (Ebel 1963, Ciesla and Franklin 1965, Coyne 1968, Merkel 1974). Keys for insect identification, descriptions of damage symptoms, and prescriptions for control with insecticides are given by DeBarr and Merkel (1971), Dinus and Yates (1975), and Ebel and others (1975). Southern cone rust, caused by *Cronartium strobilinum* Hedgc. & Hahn, reduces seed production, particularly in coastal areas. Infected cones also provide favorable habitats for *Dioryctria* species (Merkel 1958). Occurrence can be minimized by locating orchards away from hazardous areas or concentrations of evergreen *Quercus* species, the alternate hosts. Control can otherwise be had by fungicidal application during the time of natural pollination (Hepting and Matthews 1970). Some protection is also provided by pollination bags.

Significant numbers of cones are frequently destroyed by squirrels. Losses can be minimized by placing aluminum sleeves around the stems of individual ramets. Procedures are described by Krugman and Echols (1963).

Certain cultural practices—cultivation, sub-soiling, fertilization, and irrigation—offer considerable promise for increasing and maintaining seed yields. Much research has been done in seed orchards of other species (Schmidtling 1974, Davey 1975). Some encouraging results have been achieved with longleaf pine in natural stands. Fertilization alone, for example, gave fourfold to twelvefold increases in recoverable cones (Allen 1953). Fertilization and irrigation resulted in an average of 62 cones per tree as compared to only two cones per control tree (Gemmer 1932). Shoulders (1967, 1968) obtained 324 strobili per tree in response to cultivation and fertilization—a potential increase of 85 bushels of cones per acre above the yield of control trees. He also noted that the number of female strobili is influenced by rainfall amounts before initiation, production in the second year preceding initiation, and genetic differences. Fertilization and irrigation failed to increase cone yields in only one experiment (Croker 1964). Yields from trees with an inherently low potential for productivity generally are not increased by fertilization (Allen 1953, Shoulders 1967, 1968).

Treatments such as pruning, bending, and girdling have also been tested. Partial girdling of branches increased number of male strobili eightfold, but female strobili were not affected, possibly because they were naturally abundant (Varnell 1970). Partial stem girdles increased cone production and doubled seed yields (Mann and Russell 1957). Though interesting from a research standpoint, the practical value of such treatments is dubious; effects on continued seed production are most likely detrimental.

RESEARCH NEEDS

The potential of longleaf pine as well as areas and sites most suitable for its application are best clarified by new species-site trials. Particular attention should be given to sites where performance of loblolly and slash pine is marginal. Such tests should include improved materials and should incorporate the latest cultural practices.

Further evaluation of nursery, regeneration, and cultural practices is necessary, as the choice of breeding strategy depends upon the regimes eventually adopted. Problems with survival and early growth can be remedied in part by genetic manipulation and in part by cultural treatment. The two approaches must be combined in future research so as to quantify their cumulative effects.

Joint research is especially important in connection with brown-spot needle blight. In the western part of the species range, the disease is a continual threat, and site preparation that exposes the soil tends to increase incidence. Resistant strains therefore are an important objective, as is investigation of cultural practices that foster growth but retard disease spread. More research is needed to determine how much of a threat the disease is in the eastern part of the range and whether breeding for resistance is warranted in that area. Resistance breeding would also benefit from creation of a testing facility employing rapid, reliable methods of artificial inoculation.

Improvement can be obtained over much of the range by planting seed or selecting trees from the central Gulf Coast. Despite the attractiveness of such materials, boundaries of the source area remain uncertain. Efforts to delineate the area and preserve valuable germ plasm should be undertaken before the remaining forests are further reduced by logging or other activities. Application would also be hastened by more intensive testing on a broader array of sites.

Heritabilities and genetic correlations have been computed for a number of traits. Most such estimates were derived from a limited number of experiments with trees from a small segment of the species range. These estimates should be confirmed and expanded. The efficacy of indirect selection for traits with low heritabilities also deserves increased attention. Can survival and early growth, for example, be improved by indirect selection or manipulating seedling psysiology? As more information accumulates, individual traits can be weighed more realistically in existing selection guides and, eventually, in selection indices.

Lastly, much information about the genetics of longleaf pine can be obtained from new crossing experiments involving different seed sources within the species as well as with other species in Subsection *Australes*. Techniques such as electrophoresis will also be useful for acquiring information on population structure.

LITERATURE CITED

Allen, P. H.
1961. Florida longleaf pine fail in Virginia. J. For. 59:453–454.

Allen, R. M.
1953. Release and fertilization stimulate longleaf pine cone crop. J. For. 51:827.

Allen, R. M.
1958. A study of the factors affecting height growth of longleaf pine seedlings. Ph.D. diss. Duke Univ., Durham. 130 p.

Allen, R. M., and J. F. Coyne.
1956. Insect problems in forest-tree genetics. J. For. 54:193.

Barnett, J. P., and B. F. McLemore.
1970. Storing southern pine seeds. J. For. 68:24–27.

Belcher, E. W., Jr.
1973. Radiography in tree seed analysis has new twist. Tree Planters' Notes 24(3):1–5.

Bethune, J. E., and E. R. Roth.
1960. Source of seed affects growth of longleaf pine—fifth-year results. USDA For. Serv. Southeast. For. Exp. Stn. Res. Note 146, 2 p. Asheville, N.C.

Boyer, W. D.
1966. Longleaf pine pollen dispersal. For. Sci. 12:367–368.

Boyer, W. D.
1968. Foliage weight and stem growth of longleaf pine. USDA For. Serv. Res. Note SO–86, 2 p. South. For. Exp. Stn., New Orleans, La.

Boyer, W. D.
1969. The influence of temperature on date and duration of pollen shed by longleaf pine. Ph.D. thesis. Duke Univ., Durham. 171 p.

Boyer, W. D.
1972. Brown-spot resistance in natural stands of longleaf pine seedlings. USDA For. Serv. Res. Note SO–142, 4 p. South. For. Exp. Stn., New Orleans, La.

Boyer, W. D.
1973. Air temperature, heat sums, and pollen shedding phenology of longleaf pine. Ecology 54:420–426.

Boyer, W. D.
1974. Longleaf pine cone production related to pollen density. *In* Seed yield from southern pine seed orchards. p. 8–14. J. Kraus, ed. Proc., Colloq. Ga. For. Res. Counc., Macon, Ga.

Boyer, W. D., and S. R. Evans.
1967. Early flowering in longleaf pine related to seed source. J. For. 65:806.

Boyer, W. D., and F. W. Woods.
1973. Date of pollen shedding by longleaf pine advanced by increased temperatures at strobili. For. Sci. 19:315–318.

Brown, C. L.
1964. The seedling habit of longleaf pine. Ga. For. Res. Counc. Rep. 10, 68 p.

Brown, C. L.
1967. The application of tissue culture techniques to various problems in forest tree improvement. *In* Proc., Ninth South. Conf. For. Tree Improv., p. 108–110.

Buijtenen, J. P. van.
1965. Thirteenth progress report of cooperative forest tree improvement program. Tex. For. Serv. Circ. 98, 11 p.

Buijtenen, J. P. van.
1969. Seventeenth progress report of the cooperative forest tree improvement program. Tex. For. Serv. Circ. 200, 14 p.

Callaham, R. Z., and R. J. Steinhoff.
1966. Pine pollens frozen five years produce seed. *In* Joint Proc., Second Genet. Workshop Soc. Am. For. and Seventh Lake States For. Tree Improv. Conf. 1965. USDA For. Serv. Res. Pap. NC–6, p. 94–101. North Cent. For. Exp. Stn., St. Paul, Minn.

Campbell, T. E., J. M. Hamaker, and D. M. Schmitt.
1969. Longleaf pine × shortleaf pine—a new hybrid. Torrey Bot. Club Bull. 96:519–524.

Campbell, T. E., and P. C. Wakeley.
1961. Possible refinements in controlled pollination of southern pines. *In* Proc., Sixth South. Conf. For. Tree Improv., p. 121–128.

Chapman, H. H.
1922. A new hybrid pine (*Pinus palustris* × *Pinus taeda*). J. For. 20:729–734 + plate.

Chapman, W. L.
1971. The tree improvement program in Alabama—1971. Ala. For. Prod. 14(7):11, 14–15.

Ciesla, W. M., and R. T. Franklin.
1965. A survey of seed and cone insects in a South Carolina seed production area using a hydraulic lift vehicle. U.S. Dep. Agric., For. Serv., Div. State and Priv. For., Asheville, N.C. Rep. 65–1–23, 10 p.

Coker, W. C., and H. R. Totten.
1934. Trees of the southeastern states. 399 p. Univ. N.C. Press, Raleigh, N.C.

Collins, A. B., III.
1964. Longleaf pine seed source planting in Georgia. USDA For. Serv. Res. Note SE–19, 3 p. Southeast. For. Exp. Stn., Asheville, N.C.

Cool, B. M., N. B. Goebel, T. E. Wooten, and C. B. Loadholt.
1971. Glaze damage to pine trees in the sandhills area of South Carolina. Clemson Univ. Dep. For. Res. Ser. 21, 14 p.

Coyne, J. F.
1968. *Laspeyresia ingens*, a seedworm infesting cones of longleaf pine. Ann. Entomol. Soc. Am. 61:1116–1122.

Critchfield, W. B.
1963. Hybridization of the southern pines in California. *In* Proc., For. Genet. Workshop 1962, p. 40–48. Macon, Ga.

Croker, T. C., Jr.
1964. Fruitfulness of longleaf trees more important than culture in cone yield. J. For. 62:822–823.

Croker, T. C., Jr.
1971a. Binocular counts of longleaf pine strobili. USDA For. Serv. Res. Note SO–127, 3 p. South. For. Exp. Stn., New Orleans, La.

Croker, T. C., Jr.
1971b. Female strobilus stages of long leaf pine. J. For. 69:98–99.

Croker, T. C., Jr.
1973. Longleaf pine cone production in relation to site index, stand age, and stand density. USDA For. Serv. Res. Note SO–156, 3 p. South. For. Exp. Stn., New Orleans, La.

Croker, T. C., Jr.
1974. Spring and summer counts of longleaf pine seeds per cone related to October yields. Tree Planters' Notes 25(4):10.

Cumming, W. C., and F. I. Righter.
1948. Methods used to control pollination of pines in the Sierra Nevada of California. U.S. Dep. Agric. Circ. 792, 18 p.

Davey, C. B.
1975. Increasing seed yield through cultural practices—today and tomorrow. *In* Proc., Thirteenth South. For. Tree. Improv. Conf., p. 138–144.

Davis, T. S.
1962. Effect of Cobalt-60 gamma radiation on pine seed and one-year-old seedlings. For. Sci. 8:411–412.

DeBarr, G. L., and E. P. Merkel.
1971. Mist blower spraying of longleaf pine for cone and seed insect control. USDA For. Serv. Res. Pap. SE–76, 7 p. Southeast. For. Exp. Stn., Asheville, N.C.

Derr, H. J.
1963. Brown-spot resistance among F_1 progeny of a single, resistant longleaf parent. *In* Proc., For. Genet. Workshop 1962, p. 16–17. Macon, Ga.

Derr, H. J.
1966. Longleaf × slash hybrids at age 7: survival, growth, and disease susceptibility. J. For. 64:236–239.

Derr, H. J.
1971. Brown-spot resistance among progenies of longleaf plus trees. *In* Proc., Eleventh South. Conf. For. Tree Improv., p. 45–51.

Derr, H. J., and T. W. Melder.
1970. Brown-spot resistance in longleaf pine. For. Sci. 16:204–209.

Dillon, E. S., and B. J. Zobel.
1957. A simple test for viability of pine pollen. J. For. 55:31–32.

Dinus, R. J., and H. O. Yates, III.
1975. Protection of seed orchards. *In* Seed orchards. Roy Faulkner, ed. For. Comm. Bull. 54, p. 58–71, London.

Dorman, K. W.
1947. Longleaf pine cuttings rooted in greenhouse. J. For. 45:594.

Dorman, K. W.
1966. Forest tree improvement research in the south and southeast. USDA For. Serv. Res. Pap. SE–22, 90 p. Southeast. For. Exp. Stn., Asheville, N.C.

Dorman, K. W.
[In press.] The genetics and breeding of southern pines. U.S. Dep. Agric., Agric. Handb.

Dorman, K. W., and J. C. Barber.
1956. Time of flowering and seed ripening in southern pines. USDA For. Serv. Southeast. For. Exp. Stn. Pap. 72, 15 p. Asheville, N.C.

Ebel, B. D.
1963. Insects affecting seed production of slash and longleaf pines—their identification and biological annotation. USDA For. Serv. Southeast. For. Exp. Stn. Pap. SE–6, 24 p. Asheville, N.C.

Ebel, B. H., T. H. Flavell, Loyd E. Drake, and others.
1975. Seed and cone insects of southern pines. USDA For. Serv. Gen. Tech. Rep. SE–8, 40 p. Southeast. For. Exp. Stn., Asheville, N.C., and Southeast. Area, State & Private For., Atlanta, Ga.

Eggler, W. A.
1961. Stem elongation and time of cone initiation in southern pines. For. Sci. 7:149–158.

Ferré, Y. de.
1958. 'Etude d'une plantule anormale de *Pinus palustris*. Soc. d'Hist. Natur. de Toulouse Bull. 91(¾): 416–417.

Ferré, Y. de.
1965. Structure des plantules et systematique du genre *Pinus*. Soc. d'Hist. Natur. de Toulouse Bull. 100:230–261.

Franklin, E. C., and E. B. Snyder.
1971. Variation and inheritance of monoterpene composition in longleaf pine. For. Sci. 17:178–179.

Gansel, C. R.
1973. Improved techniques developed for grafting slash and longleaf pine. Tree Planters' Notes 24(2):29–32.

Gemmer, E. W.
1932. Well-fed pines produce more cones. For. Worker 8(5):15.

Goddard, R. E.
1967. Development of grafting and pollination methods. *In* Proc., Ninth South. Conf. For. Tree Improv., p. 10–14.

Goddard, R. E., C. A. Hollis III, H. R. Kok, and others.
1973. Cooperative forest genetics research program. Fifteenth Prog. Rep. Univ. Fla. Sch. For. Res. Rep. 21, 18 p.

Goddard, R. E., R. K. Strickland, and W. J. Peters.
1963. Cooperative forest genetics research program. Fifth Prog. Rep. Univ. Fla. Sch. For. Res. Rep. 9, 15 p.

Grigsby, H. C.
1969. Exotic trees unsatisfactory for forestry in southern Arkansas and northern Louisiana. USDA For. Serv. Res. Note SO–92, 5 p. South. For. Exp. Stn., New Orleans, La.

Hare, R. C.
1965. Breaking and rooting of fascicle buds in southern pines. J. For. 63:544–546.

Hare, R. C.
1974. Chemical and environmental treatments promoting rooting of pine cuttings. Can. J. For. Res. 4:101–106.

Hare, R. C.
1975. Girdling promotes rooting of slash pine cuttings. *In* Proc., Thirteenth South. For. Tree Improv. Conf., p. 226–229.

Harkin, D. A.
1957. Every seedling from selected seed. J. For. 55:842–843.

Henry, B. W., and O. O. Wells.
1967. Variation in brown-spot infection of longleaf pine from several geographic sources. USDA For. Serv. Res. Note SO–52, 4 p. South. For. Exp. Stn., New Orleans, La.

Hepting, G. H., and F. R. Matthews.
1970. Southern cone rust. USDA For. Serv., For. Pest Leafl. 27, 4 p.

Herty, C. H., and W. C. Dickson.
1908. The volatile soil of *Pinus serotina*. J. Am. Chem. Soc. 30:872–874.

Hesseltine, C. W., and E. B. Snyder.
1958. Attempts to freeze-dry pine pollen for prolonged storage. Torrey Bot. Club Bull. 85:134–135.

Hoekstra, P. E.
1957. A case study of species comparison on flatwoods soil. South. Lumberman 195 (2441) :158–159.

Johansen, R. W., and J. F. Kraus.
1958. Propagation techniques applicable to longleaf pine. J. For. 56:664.

Keng, H., and E. L. Little, Jr.
1961. Needle characteristics of hybrid pines. Silvae Genet. 10:131–146.

Kraus, J. F.
1963. The Olustee arboretum—performance of 67 species of forest trees. USDA For. Serv. Res. Pap. SE–4, 47 p. Southeast. For. Exp. Stn., Asheville, N.C.

Kraus, J. F., and D. L. Hunt.
1970. Fresh and stored pollen from slash and loblolly pines compared for seed yields. USDA For. Serv. Res. Note SE–143, 5 p. Southeast. For. Exp. Stn., Asheville, N.C.

Krugman, S. L., and R. M. Echols.
1963. Modified tree band to foil cone-harvesting squirrels. USDA For. Serv. Res. Note PSW–35, 6 p. Pacific Southwest. For. and Range Exp. Stn., Berkeley, Calif.

Lightle, P. C.
1969. Brown-spot needle blight of longleaf pine. USDA For. Serv., For. Pest. Leafl. 44 rev., 7 p.

Little, E. L., Jr., and W. B. Critchfield.
1969. Subdivisions of the genus *Pinus* (pines). U.S. Dep. Agric., Misc. Publ. 1144, 51 p.

Long, E. M.
1973. Performance of interspecific hybrids and exotic pines in Texas. *In* Proc., Twelfth South. For. Tree Improv. Conf., p. 293–301.

McCormick, J. F., and R. E. McJunkin.
1965. Interactions of gamma radiation and other environmental stresses upon pine seeds and seedlings. Health Physiog. 11:1643–1652.

McKellar, A. D.
1942. Ice damage to slash pine, longleaf pine, and loblolly pine plantations in the Piedmont section of Georgia. J. For. 40:794–797.

McLemore, B. F.
1961a. Hila of full and empty longleaf pine seeds are distinguishable. For. Sci. 7:246.

McLemore, B. F.
1961b. Storage of longleaf pine seed. Tree Planters' Notes 47:15–19.

McLemore, B. F.
1962. Predicting seed yields of southern pine cones. J. For. 60:639–641.

McLemore, B. F.
1965. Pentane flotation for separation full and empty longleaf pine seeds. For. Sci. 11:242–243.

McLemore, B. F., and H. J. Derr.
1965. Longleaf pine cone maturity is independent of pollination date. Silvae Genet. 14:133.

Maki, T. E.
1952. Local longleaf seed years. J. For. 50:321–322.

Mann, W. F., Jr.
1969. At last—longleaf can be planted successfully. For. Farmer 28:6–7, 18–19.

Mann, W. F., Jr., and T. E. Russell.
1957. Longleaf cone production doubled by ringing Tree Planters' Notes 28:6–7.

Mathews, A. C.
1932. The seed development in *Pinus palustris*. Elisha Mitchell Sci. Soc. J. 48:101–118.

Mergen, F.
1953. Gum yields in longleaf pine are inherited. USDA For. Serv. Southeast. For. Exp. Stn. Res. Note 29, 2 p. Asheville, N.C.

Mergen, F.
1954. Improving the early growth of longleaf pine. For. Farmer 13 (11) :8–9, 16–17, 19.

Mergen, F.
1958. Genetic variation in needle characteristics of slash pine and in some of its hybrids. Silvae Genet. 7:1–9.

Mergen, F., H. Rossoll, and K. B. Pomeroy.
1955. How to control the pollination of slash and longleaf pine. USDA For. Serv. Southeast. For. Exp. Stn. Pap. 58, 14 p. Asheville, N.C.

Mergen, F., G. R. Stairs, and E. B. Snyder.
1963. Microsporogenesis in *Pinus echinata* and *Pinus taeda*. Silvae Genet. 12:127–129.

Merkel, E. P.
1958. *Dioryctria* cone moth attack as related to cone rust of slash pine in north Florida. J. For. 56:651.

Merkel, E. P.
1974. Impact of cone and seed insects on slash and longleaf pines. *In* Seed yield from southern pine seed orchards. J. Kraus, ed. p. 21–25. Proc., Colloq. Ga. For. Res. Counc., Macon, Ga.

Mirov, N. T.
1961. Composition of gum turpentines of pines. U.S. Dep. Agric. Tech. Bull. 1239, 158 p.

Mitchell, H. L.
1962. Wood quality. *In* Eleventh Annu. For. Symp. La. State Univ., Baton Rouge, La., p. 10–15.

Mitchell, H. L.
1964. Patterns of variation in specific gravity of southern pines and other coniferous species. TAPPI 47:276–283.

Mohr, C.
1896. The timber pines of the southern United States. U.S. Dep. Agric. Div. For. Bull. 13, 160 p.

Namkoong, G.
1966. Statistical analysis of introgression. Biometrics 22:488–502.

North Carolina State University.
1974. Eighteenth annual report. Coop. Tree Improv. and Hardwood Res. Programs, Sch. For. Resour., N.C. State Univ., Raleigh, 95 p.

Parker, J.
1959. Seasonal variations in sugars of conifers with some observations on cold resistance. For. Sci. 5: 56–63.

Parker, J.
1965. The ability of warm-climate pines to become cold hardy. Pak. J. For. 15:156–160.

Perry, T. O., and C-W Wang.
1957a. Collection, shipping, and storage of slash and loblolly pine cuttings. J. For. 55:122–123.

Perry, T. O., and C-W Wang.
1957b. Cooperative forest genetics research program. Univ. Fla. Sch. For. Res. Rep. 4, 27 p.

Pessin, L. J.
1938. The effect of vegetation on the growth of longleaf pine seedlings. Ecol. Monogr. 8:115–149.

Quijada, R. M.
1967. Variation and relationships of wood characteristics of longleaf pine in North Carolina. M.S. thesis. N.C. State Univ., Raleigh, 91 p.

Saucier, J. R., and M. A. Taras.
1966. Wood density variation among six longleaf pine seed sources grown in Virginia. J. For. 64:463–465.

Saucier, J. R., and M. A. Taras.
1969. Regional variation in specific gravity of seven pines in the Southern United States. USDA For. Serv. Res. Pap. SE–45, 16 p. Southeast. For. Exp. Stn., Asheville, N.C.

Saylor, L. C.
1967. Variability of chromosome structure and behavior in southern pine hybrids. *In* Proc., Ninth South. Conf. For. Tree Improv., p. 95–100.

Schmidtling, R. C.
1973. Intensive culture increases growth without affecting wood quality of young southern pines. Can. J. For. Res. 3:565–573.

Schmidtling, R. C.
1974. Fruitfulness in conifers: nitrogen, carbohydrate, and genetic control. *In* Proc., Third North Am. For. Biol. Workshop, p. 148–164.

Schmidtling, R. C., and N. M. Scarbrough.
1968. Graphic analysis of Erambert's hybrid. USDA For. Serv. Res. Note SO–80, 3 p. South. For. Exp. Stn., New Orleans, La.

Schmitt, D. M.
1968. Performance of southern pine hybrids in south Mississippi. USDA For. Serv. Res. Pap. SO–36, 15 p. South. For. Exp. Stn., New Orleans, La.

Schoenike, R. E., J. D. Hart, and M. D. Gibson.
1975. Growth of a nine-year-old sonderegger pine plantation in South Carolina. Silvae Genet. 24:10–11.

Schoenike, R. E., and J. G. Williams.
1975. Ten-year results of an open-pollinated progeny test of longleaf pine in South Carolina. *In* Proc., Thirteenth South. For. Tree Improv. Conf., p. 97–104.

Sherry, S. P.
1947. The potentialities of genetic research in South African forestry. Br. Emp. For. Conf., 11 p. Pietermartizburg, Union of South Africa.

Shoulders, E.
1965. Seed origin affects longleaf pine in Louisiana plantation. USDA For. Serv. Res. Note SO–19, 3 p. South. For. Exp. Stn., New Orleans, La.

Shoulders, E.
1967. Fertilizer application, inherent fruitfulness, and rainfall affect flowering of longleaf pine. For Sci. 13:376–383.

Shoulders, E.
1968. Fertilization increases longleaf and slash pine flower and cone crops in Louisiana. J. For. 66:193–197.

Shoulders, E., and T. A. Terry.
1968. Climate at the seed source affects longleaf pine performance in Louisiana plantation. USDA For. Serv. Res. Note SO–78, 4 p. South. For. Exp. Stn., New Orleans, La.

Siggers, P. V.
1955. Control of the fusiform rust of southern pines. J. For. 53:442–446.

Slade, W. L.
1971. Longleaf grafting techniques. *In* Proc., Eleventh Conf. South. For. Tree Improv., p. 230–231.

Smith, H. D., and L. F. Smith.
1969. Grafting longleaf pine. Tree Planters' Notes 19(4):21–23.

Smith, L. F.
1961. Tree percent on burned and unburned longleaf seedbeds. J. For. 59:201–203.

Smith, L. F., and R. C. Schmidtling.
1970. Cultivation and fertilization speed early growth of planted southern pines. Tree Planters' Notes 21(1):1–3.

Smith, L. F. , E. B. Snyder, and N. M. Scarbrough.
1963. Care of pine seedlings used in breeding at Institute of Forest Genetics. USDA For. Serv. Res. Note SO–2, 4 p. South. For. Exp. Stn., New Orleans, La.

Snyder, E. B.
1957. Pollen handling. *In* Proc., Fourth South. Conf. For. Tree Improv. p. 111–115.

Snyder, E. B.
1961a. Measuring branch characters of longleaf pines. U.S. Dep. Agric. For. Serv., South. For. Exp. Stn., Occas. Pap. 184, 4 p. New Orleans, La.

Snyder, E. B.
1961b. Extracting, processing, and storing southern pine pollen. U.S. Dep. Agric. For. Serv., South. For. Exp. Stn., Occas. Pap. 191, 14 p. New Orleans, La.

Snyder, E. B.
1969. Parental selection versus half-sib family selection of longleaf pine. *In* Proc., Tenth South. Conf. For. Tree Improv., p. 84–88.

Snyder, E. B.
1973. 15-year gains from parental and early family selection in longleaf pine. *In* Proc., Twelfth South. For. Tree Improv. Conf., p. 46–49.

Snyder, E. B., and R. M. Allen.
1963. Sampling, nursery, and year-replication effects in a longleaf pine progeny test. *In* Proc. Soc. Am. For. and South. For. Tree Improv. Comm. For. Genet. Workshop 1963. p. 26–27.

Snyder, E. B., and R. M. Allen.
1968. Mountain longleaf pine excels only in local plantings. USDA For. Serv. Res. Note SO–83, 4 p. South. For. Exp. Stn., New Orleans, La.

Snyder, E. B., and K. E. Clausen.
1974. Pollen handling. *In* Seeds of woody plants in the United States. U.S. Dep. Agric., Agric. Handb. No. 45, p. 75–97.

Snyder, E. B., and H. J. Derr.
1972. Breeding longleaf pines for resistance to brown-spot needle blight. Phytopathology 62:325–329.

Snyder, E. B., H. C. Grigsby, and J. U. Hidalgo.
1961. X-radiation of southern pine seed at various moisture contents. Silvae Genet. 10:125–131.

Snyder, E. B., and A. E. Squillace.
1966. Cone and seed yields from controlled breeding of southern pines. USDA For. Serv. Res. Pap. SO–22, 7 p. South. For. Exp. Stn., New Orleans, La.

Snyder, E. B., A. E. Squillace, and J. M. Hamaker.
1966. Pigment inheritance in slash pine seedlings. *In* Proc., Eighth South. Conf. For. Tree Improv. 1965, p. 77–85.

Stephenson, G. K., and E. B. Snyder.
1969. Genetic variation—key to superior trees. 12 p. USDA For. Serv. South. For. Exp. Stn., New Orleans, La.

Strickland, R. K.
1965. Longleaf pine specific gravity variation. Univ. Fla. Sch. For. Tree. Improv. Tips 11, 1 p.

Strickland, R. K.
1968. Longleaf pine growth efficiency. Univ. Fla. Sch. For. Tree Improv. Tips 15, 2 p.

Summerville, K. O., and G. F. Turner.
1973. New equipment improves pollen viability. Tree Planters' Notes 24:3–6.

U.S. Department of Agriculture, Forest Service.
1965. Southern wood density survey—1965 status report. USDA For. Serv. Res. Pap. FPL–26, 38 p. For. Prod. Lab., Madison, Wis.

U.S. Department of Agriculture, Forest Service.
1971. Forest tree seed orchards. USDA For. Serv., 15 p.

U.S. Department of Agriculture, Forest Service.
1974a. Forest tree seed orchards. U.S. Dep. Agric., For. Serv., 33 p.

U.S. Department of Agriculture, Forest Service.
1974b. Seeds of woody plants in the United States. U.S. Dep. Agric., Agric. Handb. 450, 883 p.

Van Lear, D. H., and J. R. Saucier.
1973. Comparative glaze damage in adjacent stands of slash and longleaf pine. Clemson Univ. Dep. For. Res. Ser. 27, 7 p.

Vande Linde, F.
1969. Some practical aspects of seed orchard management in the South. *In* Proc., Tenth South. Conf. For. Tree Improv., p. 199–204.

Varnell, R. J.
1970. Effects of branch girdling on the production of male and female strobili in longleaf pine. For. Sci. 16:195–196.

Verrall, A. F.
1934. The resistance of saplings and certain seedlings of *Pinus palustris* to *Septoria acicola*. Phytopathology 24:1262–1264.

Wahlenberg, W. G.
1946. Longleaf pine. Charles Lathrop Pack For. Found., Washington, D.C., 429 p.

Wahlgren, H. E., and D. R. Schumann.
1972. Properties of major southern pines. I. Wood density survey. USDA For. Serv. Res. Pap. FPL–176–177, p. 1–57. For. Prod. Lab., Madison, Wis.

Wakeley, P. C.
1927. The sins of the fathers. USDA For. Serv., Serv. Bull. 11(17):3–4.

Wakeley, P. C.
1954. Planting the southern pines. U.S. Dep. Agric., Agric. Monogr. 18, 233 p.

Wakeley, P. C.
1968. Rust susceptibility in longleaf pine associated with brown-spot resistance and early commencement of height growth. For. Sci. 14:323–324.

Wakeley, P. C.
1970. Thirty-year effects of uncontrolled brown spot on planted longleaf pine. For. Sci. 16:197–202.

Wakeley, P. C., and T. E. Campbell.
1954. Some new pine pollination techniques. USDA For. Serv. South. For. Exp. Stn. Occas. Pap. 136, 13 p., New Orleans, La.

Wakeley, P. C., and T. E. Campbell.
1960. Seedless longleaf cones can mature and open. South. For. Notes 127, 4 p. South. For. Exp. Stn., New Orleans, La.

Wells, D. W., and M. Reines.
1965. Vegetative propagation of needle bundles of pines. Ga. For. Res. Counc. Res. Pap. 26, 8 p.

Wells, O. O.
1969. Results of the Southwide Pine Seed Source Study through 1968–69. *In* Proc., Tenth South. Conf. For. Tree Improv., p. 117–129.

Wells, O. O., and P. C. Wakeley.
1970. Variation in longleaf pine from several geographic sources. For. Sci. 16:28–42.

Zak, B.
1955. The grafting of shortleaf and other pine species. USDA For. Serv. Southeast. For. Exp. Stn. Pap. 59, 13 p. Asheville, N.C.

Zobel, B. J., and R. E. Goddard.
1954. Pine flowering and seed ripening in Texas. Tex. For. Serv. Res. Note 8, 10 p.

Zobel, B. J., R. C. Kellison, M. F. Matthias, and A. V. Hatcher.
1972. Wood density of the southern pines. N.C. Agric. Exp. Stn. Tech. Bull 208, 56 p.

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WO–33, 24 p.

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